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Observations on the Distribution, Behavior, and Comparative Breeding Biology of *Neoxolmis rufiventris* (Aves: Tyrannidae)

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ABSTRACT

As many as 93–94 individuals of the relatively uncommon and highly terrestrial Chocolate-vented Tyrant *Neoxolmis rufiventris* (Vieillot, 1823) (Aves: Tyrannidae: Fluvicolinae) were encountered at 70 lowland (60–920 m) sites in Santa Cruz, Argentina, and Magallanes (Region XII), Chile, during the austral spring of 1993. Sites were typically very open and included steppes with scattered cushion plants, grass steppes, and grass-cushion plant and grass-shrub associations. Most sites (70%) held solitary birds; relatively few contained 2 (27%), 3 (1%), or 4 (1%) individuals, some of which may have been paired. No nests were found. Most sightings were in the late morning and in the afternoon and early evening, suggesting a bimodal activity pattern. Foraging on or near the ground for small prey, faint vocalizations including alarm calls emitted by an apparent pair, intraspecific aerial pursuits of 5–20 m height and up to 10 sec duration, and presumptive aerial displays, were observed. The swift, direct flight

of *N. rufiventris* resembles sympatric, predatory *Falco sparverius* (Falconidae) and *Muscisaxicola* species (Tyrannidae), a fact that may account for the mobbing reactions that the former was seen to elicit in *Geositta cunicularia* (Furnariidae) and *M. capistrata*.

Evidence of nesting in *Neoxolmis rufiventris* previously consisted of reports of three nests from Río Negro (1) and Santa Cruz (2), Argentina. Six additional nests and egg sets from Río Negro (5) and Santa Cruz (1) are described here, based on collections made by J. R. Pemberton in 1911 and by A. T. Waldron in 1933. The nine known nests were situated either in Patagonian steppe (8) or in steppe habitat within Monte (1). At ca. 775–1600 m, the Río Negro sites are geographically and altitudinally disjunct from the Santa Cruz localities, which lie at or below 100 m. Breeding takes place from late October–late December and is partly synchronous in the two provinces, though relatively late at higher elevations in Río Negro. Par-

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tial coincidence of breeding phenology, presence of steppe habitat in intervening parts of Chubut, and probable commingling of migrants on wintering grounds in northern Argentina, Uruguay, and southern Brazil, suggest potential gene flow between the Río Negro and Santa Cruz populations.

All of the known nests of the Chocolate-vented Tyrant were placed in relatively sheltered locations, either on flat or sloping ground next to a grass tussock, shrub, or rock or, in one instance, 2.4 m above ground inside a rock crevice. The nest is an open cup, usually of dry grass, some

sticks, and a lining of feathers. The clutch comprises 1–3 (modally 2) ovoidal eggs with pink or cream ground color and reddish and gray spots near the larger pole. A comparative analysis of nest site and clutch size variation in *Neoxolmis rufiventris* and 27 related species of the *Muscisaxicola* group (sensu Lanyon, 1986) suggests that open-cup tree or shrub nests are primitive for this assemblage, and that ground-nesting habits and relatively small, two-egg clutches arose independently in *Muscisaxicola* and *Neoxolmis* via separate invasions of semiarid resource-poor biotopes, respectively in the Andes and in the cis-Andean rain shadow.

RESUMEN

Durante el verano austral de 1993, un alto número (93–94) de individuos de la relativamente poco común y muy terrícola Monjita Chocolate *Neoxolmis rufiventris* (Vieillot, 1823) (Aves: Tyrannidae: Fluvicolinae) fueron hallados en 70 localidades de baja altitud en Santa Cruz, Argentina, y Magallanes (Región XII), Chile. Estas localidades constituían en su mayoría paisajes muy abiertos con vegetación que incluían estepas con escasas plantas almohadilladas, estepas de gramineas y asociaciones de gramineas-plantas almohadilladas y de gramineas-arbustos. La mayoría de las localidades (70%) tenían aves solitarias; relativamente pocas localidades tenían 2 (27%), 3 (1%) o 4 (1%) individuos, algunos de los cuales posiblemente formaban parejas. No se descubrieron nidos. La mayoría de los avistamientos se hicieron tarde en la mañana y en la tarde o en el crepúsculo, sugiriendo un patrón de actividad bimodal. Estas aves fueron observadas durante la búsqueda de pequeñas presas en o cerca del suelo, emitiendo vocalizaciones tenues incluidos gritos de alarma emitidos por una supuesta pareja, persecuciones intraespecíficas aéreas a 5–20 m de altura y de hasta 10 segundos de duración, y posibles vuelos nupciales. El rápido y directo vuelo de *N. rufiventris* se asemeja al vuelo del simpátrido predador *Falco sparverius* (Falconidae) y al de las especies de *Muscisaxicola* (Tyrannidae). Este hecho podría explicar las reacciones de persecución de *Geositta cunicularia* (Furnariidae) y *M. capistrata* iniciadas por *N. rufiventris*.

Las evidencias de nidificación en *Neoxolmis rufiventris* consistían de hallazgos de sólo tres nidos, uno en Río Negro y dos en Santa Cruz, Argentina. Aquí se describen otros seis nidos y conjuntos de huevos adicionales de Río Negro (5) y de Santa Cruz (1). Estos nuevos datos están basados en colecciones hechas por J. R. Pem-

berton en 1911 y por A. T. Waldron en 1933. De los nueve nidos conocidos, ocho provienen de la estepa patagónica y uno del hábitat de estepa en la región del Monte. Las localidades de Río Negro, a altitudes de aproximadamente 775–1600 m, están separadas geográficamente y altitudinalmente de las localidades de Santa Cruz, las que se encuentran a 100 m de altura o menos. La época de cría se extiende desde fines de octubre hasta fines de diciembre y es casi simultánea en las dos provincias, si bien ocurre algo más tarde en las elevaciones más altas de Río Negro. La coincidencia parcial de la fenología de cría, la presencia de hábitat de estepa en las zonas interpuestas de Chubut y la probable mezcla de individuos migratorios en zonas invernales en el norte de Argentina, Uruguay, y el sur de Brasil, sugieren un flujo génico potencial entre las poblaciones de Río Negro y las poblaciones de Santa Cruz.

Todos los nidos conocidos de la Monjita Chocolate estaban localizados en sitios relativamente protegidos, en suelos planos o de una suave pendiente, cercanos a campos de gramineas, arbustos, rocas o, en un caso particular, a 2,4 m de altura sobre el suelo, adentro de una pequeña cueva en la roca. El nido, con forma de taza abierta, es usualmente construido con paja seca y algunos palillos, con el lecho compuesto de plumas. La puesta contiene 1–3 (modalmente 2) huevos ovoidales de color rosado o crema, con manchas rojizas y grises cerca del polo grueso. Se llevó a cabo un análisis comparativo de la variabilidad de las localidades de anidación y del tamaño de la puesta en *Neoxolmis rufiventris* y en 27 especies emparentadas del grupo *Muscisaxicola* (sensu Lanyon, 1986). Este análisis sugiere que los nidos con forma de taza abierta, puestos en árboles o arbustos, son primitivos para este agrupamiento, y que la costumbre de anidar en el suelo y de

poner puestas relativamente pequeñas (dos huevos) se desarrolló independientemente en *Muscisaxicola* y *Neoxolmis* como resultado de inva-

siones separadas a sus respectivos biótopos, semiáridos y de pobres recursos, en los Andes y en la zona cis-Andina bajo efecto de "rain shadow."

INTRODUCTION

The Chocolate-vented Tyrant *Neoxolmis rufiventris* (Vieillot, 1823; see appendix 1), a relatively uncommon and highly terrestrial member of the *Muscisaxicola* group (Lanyon, 1986) of bush and ground tyrants (Tyrannidae: Fluvicolinae), breeds in open Patagonian steppes of central and southern Argentina during the austral spring and summer, and it undertakes a reverse (austral) migration to open grasslands and fields in northern Argentina, Uruguay, and southeastern Brazil during the fall and winter (Hudson, 1920; Hellmayr, 1925, 1927; Olrog, 1963, 1979; Belton, 1974; Contreras and Roig, 1977; Gore and Gepp, 1978; Clark, 1986; Narosky and Di Giacomo, 1993; Sick, 1993; Ridgely and Tudor, 1994; Chesser, 1994). Data on distribution, behavior, and breeding biology of this species are scarce. Published records of breeding appear limited to reports of three nests from Santa Cruz and Río Negro, Argentina (reviewed by Casas, 1996), and to a report of young from Santa Cruz (Olrog, 1963).

The breeding range of the Chocolate-vented Tyrant is hypothesized to include coastal southeastern Río Negro and northeastern Chubut, Argentina, where paired adults and solitary young have commonly been observed in January (Contreras, 1978); the southern Chilean mainland (Magallanes; Clark, 1986; Venegas, 1994) where, on 27 November 1988, Vuilleumier (1994) collected an adult male with a brood patch; and northern Tierra del Fuego (Hellmayr, 1925, 1927; Traylor, 1979; Clark, 1986; Fjeldså and Krabbe, 1990; Ridgely and Tudor, 1994), where it is said to be uncommon or rather rare (Venegas, 1994), but where irruptions reportedly occur in some years (Johnson, 1967). Humphrey et al. (1970: 268) state that "The species may be a rare summer breeding visitor [to Isla Grande, Tierra del Fuego] but until more data are available we tentatively consider it as an accidental." Jehl and Rumboll (1976: 149) postulate that *Neoxolmis ru-*

fiventris is "probably commoner [on Isla Grande] than the few records suggest."

The Chocolate-vented Tyrant is said to occur singly or in pairs while breeding, and to congregate in small to large flocks during migration and in winter (Contreras and Roig, 1977; Fjeldså and Krabbe, 1990; Ridgely and Tudor, 1994). Estimates of its relative abundance in Patagonia range from uncommon (Ridgely and Tudor, 1994) to common (Maclean, 1969); Narosky and Yzurieta (1989: 210) accord the species a "III" on a scale of I–VI, VI indicating the highest probability of being seen. Fjeldså and Krabbe (1990: 504) note that "Numbers [of *Neoxolmis rufiventris*] fluctuate greatly. Some years abundant at the Strait of Magellan and plateaus of Sta Cruz, other years almost absent." Vuilleumier (1994: 18, 24) found *N. rufiventris* to be only 0–0.25 times as abundant as its partly sympatric congener the Rusty-backed Monjita *N. rubetra* in steppes and shrub-steppes of Río Negro in 1991 and 1992, and he questioned the reported abundance fluctuations, having found *N. rufiventris* to be consistently "rare and localized" on steppes in Chilean Fuego-Patagonia in 1985, 1987, and 1988.

During an expedition to Patagonia and Tierra del Fuego in 1993, we also found *Neoxolmis rufiventris* to be rare and localized, but we succeeded in observing the species at some 70 sites from 15 November to 7 December (fig. 1, appendix 2). These observations, organized under the rubrics of "Distribution" and "Behavior," comprise the following two parts of the present paper. In a third section, entitled "Breeding," we report six hitherto unpublished egg and nest records of *N. rufiventris* from the collections of J. R. Pemberton (Wetmore, 1923, 1926b) and A. T. Waldron (appendix 3), and we interpret these in the context of previous breeding records of this species. Lastly, in a concluding section entitled "Comparative Breeding Biology," we analyze nest site preferences and

clutch sizes in *N. rufiventris* and 27 other species of the *Muscisaxicola* group in an attempt to infer some evolutionary and biogeographic trends within this rather heterogeneous Neotropical assemblage.

This paper is the fourth in a series of articles that we have authored singly or jointly on the distribution, behavior, breeding biology, and evolution of Patagonian and Andean flycatchers of the family Tyrannidae (Vuilleumier, 1971, 1994; Andors and Vuilleumier, 1996).

MATERIAL

Specimens cited herein are distinguished by the following acronyms:

AWJ	Collection of Alfred W. Johnson, Santiago de Chile, Chile (not located)
DMNH	Delaware Museum of Natural History, Wilmington, Delaware
MRDLP	Collection of Dr. Martín R. de la Peña, Esperanza, Santa Fe, Argentina
MVZ	Museum of Vertebrate Zoology, University of California, Berkeley, California
SBMNH	Santa Barbara Museum of Natural History, Santa Barbara, California
USNM	Division of Birds, National Museum of Natural History, Smithsonian Institution, Washington, D.C.
WFVZ	Western Foundation of Vertebrate Zoology, Camarillo, California

DISTRIBUTION

SITES AND HABITAT TYPES: The 70 sites at which *Neoxolmis rufiventris* was observed in 1993 (fig. 1, appendix 2) are numbered sequentially in the order visited, and are dis-

tributed by province and river system as follows: northeastern Santa Cruz, Argentina, to the north (sites 1–8) and south (9–11) of the lower Río Deseado; northwestern Santa Cruz in the upper Río Deseado watershed (67–70) and on the interfluvium between the Río Olnie and the upper Río Chico (59–66); central and eastern Santa Cruz on the left (12–15) and right (16–31, 56–58) banks of the Río Chico; southwestern Santa Cruz in the upper Río Shehuen (Chalía) (51–55), Río La Leona (50), and upper Río Coig (Coyle)–Río Pelque (39–49) drainage basins; southeastern Santa Cruz near the divide between the lower Río Santa Cruz and lower Río Coig (Coyle) (32); southeastern Santa Cruz (33–34) and eastern Magallanes (Region XII), Chile (35–37) between the lower Río Gallegos and the Estrecho de Magallanes; and northern Isla Grande (Tierra del Fuego), Magallanes on the left bank of the Río Sida (38). Observations were largely restricted to roadsides. The total distance traveled by road between sites 1 (15 November) and 70 (7 December) was 4358 km. The northernmost and southernmost sites (70 and 38, respectively) spanned ca. 6°27' of latitude and ca. 715 km. Habitats where we found *N. rufiventris* were typically very open and included barren areas with scattered cushion plants; grass steppes, including pastures, with the grasses often short and with tussocky growth habits; grass-cushion plant (fig. 2) or grass-shrub associations; and dense shrubsteppe. All 70 sites are situated within Hueck and Seibert's (1981) Patagonian steppe and semidesert phytogeographic region (fig. 1).

NUMBER OF INDIVIDUALS: A few individuals of *Neoxolmis rufiventris* may have been counted twice at some sites (16–26) in the case of one road (Ruta 2310, between Go-

→

Fig. 1. Sight (1–70, ○) and breeding records (71–79, ■) of *Neoxolmis rufiventris* in southern South America (Argentina and Chile), based on the American Museum of Natural History Patagonia Expedition of 1993 (1–70), eggs collected by J. R. Pemberton in 1911 (71–75) and by A. T. Waldron in 1933 (76), and previously published nest records (77–79). Base map compiled from Automóvil Club Argentino Publs. 905 (Río Negro), 801 (Chubut), 947 (Santa Cruz), and 825 (Tierra del Fuego), with simplified hydrography and phytogeographic regions (Monte shrubsteppe, pink; Patagonian steppes and semideserts, yellow; after Hueck and Seibert, 1981) shown only for parts of southern Argentina (Río Negro, Chubut, Santa Cruz, Tierra del Fuego) and Chile (Magallanes). See appendix 2 and text for details.



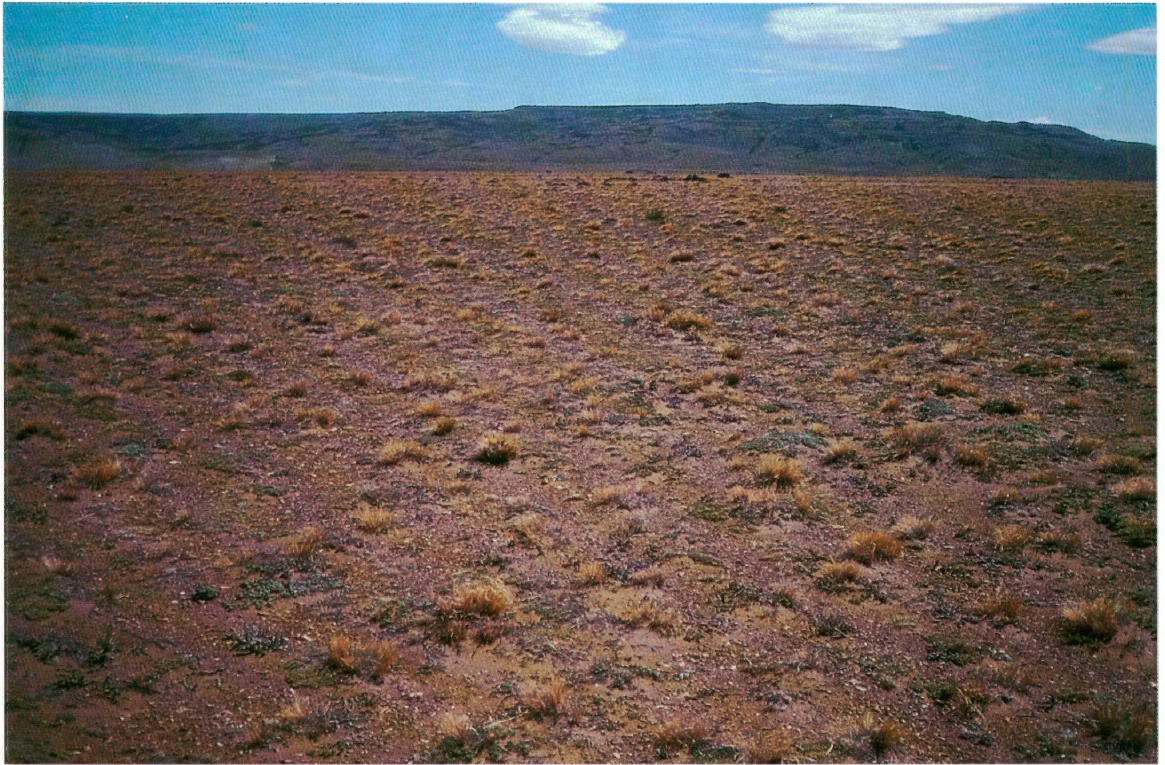


Fig. 2. Overgrazed short grass-cushion plant steppe in the Río Chico valley at site 27, central Santa Cruz, Argentina (fig. 1; appendix 2). A probable pair of *Neoxolmis rufiventris* was observed foraging in this area on 21 November 1993. Photograph by F. Vuilleumier.

bernador Gregores and Lago Cardiel) that was traversed in both directions on the same day (19 November). Thus, the figure 93–94 is probably a slight overestimate of the total number of individuals of *N. rufiventris* that were seen (table 1, appendix 2).

INCIDENCE OF PAIRING: On its breeding grounds in western Río Negro, *Neoxolmis rufiventris* is said to “usually [occur] in pairs or bands of three or four” individuals (Pemberton, MS). By contrast, the majority (49 out of 70, or 70%) of our sightings in Santa Cruz and Magallanes were of solitary birds (table 1, appendix 2). Relatively few sites were inhabited by duos (27%), trios (1%), or quartets (1%). Duos that were either flushed together (site 28), seen standing (61), foraging (1, 2, 27), or flying (45) in proximity, or observed in intraspecific aerial chases (3, 8, 12) or in aerial displays (1, 50) may have been paired. Pairing could not, however, be demonstrated unequivocally. At one site

(65), four individuals, including two apparent fledglings, were observed together in a presumptive family group (see “Intraspecific Interactions”).

ELEVATIONAL RANGE: Of the 55 sites at which elevation above sea level was estimated with an altimeter, the majority (45, or 82%) were between 200–800 m, and most (36, or 65%) were below 500 m (table 1, appendix 2). Similarly, Ridgely and Tudor (1994: 609) note that *Neoxolmis rufiventris* occurs “Mostly below 500 m.”

BEHAVIOR

ACTIVITY PATTERNS: Peak numbers of sightings of *Neoxolmis rufiventris* were made in the late morning (10:00–11:59 hr) and in the afternoon and early evening (14:00–19:59 hr), possibly indicating a bimodal activity pattern of the birds (or, conceivably, of the observers) for those 51 sites at which the

TABLE 1
Frequency Distributions^a

No. of birds	f	Elevation (m)	f	Time (hr)	f
1	49	0–199	9	10:00–11:59	11 ^d
2	19	200–399	15	12:00–13:59	9 ^e
3	1 ^b	400–599	14	14:00–15:59	5
4	1 ^c	600–799	15	16:00–17:59	11
		800–999	2	18:00–19:59	11
				20:00–21:59	4

^a Number of individuals of *Neoxolmis rufiventris* per site and number of sites per 200 m or 2 hr interval; f denotes frequency. Data from appendix 2.

^b Site 28, 2–3 birds.

^c Site 65.

^d Includes site 27, 11:30–13:00 hr.

^e Omits site 27.

time of day was recorded (table 1, appendix 2).

FORAGING: Foraging for small prey, observed mostly in the evening at only a few sites (1, 2, 4, 27, 42), took place semiterrestrially or terrestrially in the manner described by Crawshaw (1907: 61), Fjeldså and Krabbe (1990: 503–504), and Vuilleumier (1994: 22, 24). In the one instance in which we saw a Chocolate-vented Tyrant capture a prey item (at site 42), the latter was minute and unidentifiable.

VOCALIZATIONS: *Neoxolmis rufiventris* was heard calling faintly at three sites at midday (33) and in the early evening (28, 30), in high winds that precluded analysis of the calls (described by Hudson, 1920; Fjeldså and Krabbe, 1990; Straneck, 1990; Ridgely and Tudor, 1994; and Vuilleumier, 1994). At site 28, an apparent pair emitted alarm calls after they were flushed from an area of low grass tussocks.

INTRASPECIFIC INTERACTIONS: As noted by Hudson (1920: 137) and Ridgely and Tudor (1994: 608), individuals of *Neoxolmis rufiventris* often chase each other in the air. At each of three sites (3, 8, 12), we observed an aerial pursuit of one Chocolate-vented Tyrant by another. Two of these pursuits reached heights of ca. 5 m (12) and 20 m (3), and one lasted ca. 10 sec (3). At two other sites (1, 50), one bird sallied upwards from the ground to a height of ca. 5 m (1) or 6–7 m (50) while another individual, perhaps its

mate, stood nearby. We tentatively interpret these sallies as aerial displays, as neither one appeared to involve prey capture. Two members of a family quartet at site 65 exhibited hunched begging postures suggestive of fledglings.

INTERSPECIFIC INTERACTIONS: *Neoxolmis rufiventris* has been likened in shape and behavior to a turdid thrush (Crawshaw, 1907; Pemberton, MS; Hudson, 1920; Fjeldså and Krabbe, 1990; Venegas, 1994) or, perhaps more aptly, to a large *Muscisaxicola* ground-tyrant or to the sympatric American Kestrel *Falco sparverius* (Falconidae; Ridgely and Tudor, 1994), which may occasionally prey on small passeriform birds (White, 1994). As noted by Ridgely and Tudor (1994: 608), its “Flight is very swift and direct with pointed wing shape almost like a falcon’s.” This resemblance of the Chocolate-vented Tyrant to a falcon or to a *Muscisaxicola* ground-tyrant may explain the defensive, mobbing reaction that we saw elicited in the Common Miner *Geositta cunicularia* (Furnariidae), one individual of which pursued a solitary *Neoxolmis rufiventris* at site 56, and in the Cinnamon-bellied Ground-Tyrant *Muscisaxicola capistrata*, one of which mobbed one of two *N. rufiventris* at site 61.

BREEDING

PREVIOUS RECORDS: The three previously published nesting records of *Neoxolmis rufiventris*, recently summarized by Casas (1996), are listed in synoptic fashion in appendix 2 (77–79) and are mapped in figure 1 (77–79) with respect to vegetation. The first and second reported nests, from Estancia Las Vegas (77; Maclean, 1969, 1972, 1974) and Puerto Deseado (78; de la Peña, 1985, 1987, 1988), Santa Cruz, were both situated within Patagonian steppe and semidesert (Hueck and Seibert, 1981). Gordon L. Maclean (personal commun.) describes the habitat of the Estancia Las Vegas site as “bleak, windswept, flat upland, with sparse grass, some low woody shrubs and some very widely scattered taller bushes of *Berberis buxifolia*” (Berberidaceae). The third reported nest, from ca. 20 km east of El Cañ, south central Río Negro (79; Vuilleumier, 1994), was placed in open “steppe” with low

shrubs (including *Mulinum spinosum*, Umbelliferae), grass tussocks (dominated by *Festuca* sp., Gramineae), and bare areas of soil within the Monte phytogeographic region (Hueck and Seibert, 1981).

The nest at Estancia Las Vegas (fig. 3), studied by Maclean on 3–4 December 1967, contained a clutch of three eggs (table 2, AWJ) with one incubating parent bird in attendance. The nest at Puerto Deseado, found by de la Peña on 7 November 1979, contained one nestling and two unincubated eggs (table 2, MRDLP 379). The nest from Río Negro, discovered by Vuilleumier on 7 November 1992, contained two large young and had two parent birds in attendance (not collected). These three nest records are considered in greater detail below (see “Generalizations”).

ADDITIONAL RECORDS: Río Negro: Kiff and Hough (1985: 107; see also Lanyon, 1986: 51; Vuilleumier, 1994: 13) appear to have been the first to cite the presence of five sets of eggs of *Neoxolmis rufiventris* in the Western Foundation of Vertebrate Zoology (four sets: WFFVZ 15164–15167) and the Santa Barbara Museum of Natural History (one set: SBMNH 166-25). These were collected in 1911 in southwestern Río Negro (fig. 1, 71–75) by or for John Roy Pemberton (1884–1968), a noted American petroleum geologist, ornithologist, and founder of the WFFVZ (Harrison and von Bloeker, 1972), whose 1911–1915 Patagonian bird-skin collection in the Museum of Vertebrate Zoology, Berkeley—made while engaged in geological field work for the Argentine Comisión de Estudios Hidrológicos—was reported upon by Wetmore (1923, 1926b). According to Lloyd F. Kiff (personal commun.), “The data on the eggs [in the Pemberton collection] were never published, but Pemberton did prepare an ms. on his nesting observations which is still at the Western Foundation [(Pemberton, MS)] . . . Pemberton gave his Patagonian eggs to the WFFVZ in its early years of existence, but he had already given a pretty good sampling of the eggs to William Leon Dawson . . . when the latter . . . started the ‘Museum of Comparative Oology’ (now the . . . Santa Barbara Museum of Natural History).” Measurements and other data on Pemberton’s collection of eggs of *N.*

rufiventris are presented in table 2 and in appendixes 2 (71–75) and 3.

Pemberton’s identification of his first set of eggs of *Neoxolmis rufiventris* (WFFVZ 15164), which was collected by a “Peon” on 1 November 1911, was a posteriori and based on his having personally flushed a bird from a subsequent nest, on 9 November 1911 (WFFVZ 15165). By 10 November 1911, the eggs of this species were familiar to him, for he noted on a set slip (WFFVZ 15166), “Bird described & eggs known by m[e]” (appendix 3). Determinations of later sets were based either on sight identification of a flushed bird, on 23 December 1911 (SBMNH 166-25), or, in the case of a “deserted nest” with an addled egg collected on 31 December 1911 (WFFVZ 15167), on familiarity with the nest and egg. All five sets were cross-referenced to two voucher skins of *N. rufiventris* that Pemberton collected at Arroyo Seco, Río Negro on 2 and 6 September 1911, and which he referred to on his set slips as “#76” (“76A” on skin label = MVZ 42972) and “77” (“77A” on skin label = MVZ 42973), respectively (Wetmore, 1926b: 447; Carla Cicero, personal commun.). All five sets are similar inter se and appear to have been correctly identified on the corresponding set slips as “*Myiotheretes* [= *Neoxolmis*] *rufiventris*” (Walter Wehtje, personal commun.; personal obs.), to judge from photographs of these five sets (unpubl.) and of another, hitherto unreported set (fig. 4), as well as from descriptions and illustrations of two other, evidently conspecific sets published respectively by Maclean (1969, 1972, 1974) and de la Peña (1985, 1987, 1988).

Although labeled originally—apparently by Pemberton—as “Chocolate Ground Tyrant *Myiotheretes rufiventris* (Vieillot),” the set slip of SBMNH 166-25 was subsequently, and without explanation, relabeled by someone else as “Rufous-naped Ground Tyrant *Muscisaxicola rufivertex*.” This reidentification seems erroneous for several reasons: (a) *Muscisaxicola rufivertex* is not known to breed in southwestern Río Negro where Pemberton collected SBMNH 166-25 (Fjeldså and Krabbe, 1990; Ridgely and Tudor, 1994). (b) The two eggs comprising SBMNH-166-25 (table 2) are each substantially larger than an egg of *Muscisaxicola ru-*

TABLE 2
Clutch Sizes and Dimensions (in mm) of Eggs of *Neoxolmis rufiventris*^a

Specimen No.	Clutch size	Length × Breadth	Source
AWJ ^b	3	28.0 × 21.4	1
		28.7 × 21.4	1
		28.2 × 21.5	1
DMNH 23722	2	31.6 × 21.6	2
		29.4 × 21.2	2
MRDLP 379 ^c	2	30.8 × 23	3
		31 × 22.8	3
SBMNH 166-25	2	28.62 × 20.44	4
		28.70 × 20.36	4
WFVZ 15164	2	31.26 × 20.46	5
		31.64 × 20.80	5
WFVZ 15165	2 ^d	32.22 × 20.25	5
WFVZ 15166	2 ^d	29.48 × 21.02 ^e	5
WFVZ 15167	1	31.43 × 21.10	5
Range	1–3	28.0–32.22 × 20.25–23	2
Mean	2.0	30.08 × 21.24	2
SD	0.5345	1.4813 0.8342	2

^a SD, standard deviation of sample.

^b Formerly in Alfred W. Johnson collection, Santiago de Chile, Chile (Maclean, 1969: 145). Present location unknown.

^c Assigned No. 1520790 by Lloyd F. Kiff.

^d One egg broken and not measured.

^e Cracked but measurable.

Note—Sources of data are as follows:

1—Maclean (1969: 145).

2—This paper.

3—de la Peña (1985: 13).

4—Krista A. Fahy (personal commun.).

5—Clark Sumida (personal commun.).

rufiventris in the National Museum of Natural History (USNM 16352; 21.0 × 15.1 mm), and are larger than eggs of *M. rufiventris* *achalensis* (including “*pallidiceps*”) reported in the literature (24.2 × 16.9, 24.0 × 17.1, 23.7 × 16.6 mm; Salvador and Narosky, 1984; Salvador and Salvador, 1988). (c) Photographs of SBMNH 166-25 compare more or less favorably with published illustrations of eggs of *Neoxolmis rufiventris* (de la Peña, 1985, 1987) and, as mentioned, with photographs of WFVZ 15164–15167 (personal obs.), although the eggs comprising SBMNH 166-25 are smaller and more pyriform, and are marked with relatively smaller spots, than a representative WFVZ set (Walter Wehtje, personal commun.; personal obs.). These differences can be tentatively ascribed to intra-

specific variation, since the dimensions of SBMNH 166-25 fall within the known size range of eggs of *N. rufiventris* (table 2). (d) Pemberton collected SBMNH 166-25 personally after having flushed a bird from the nest. He was by this time (23 December 1911) quite familiar with *N. rufiventris*, based on his having previously collected three voucher skins (MVZ 42972–42974; Wetmore, 1926b: 447) and three other sets of eggs of this distinctive species. (e) Similarities between the generic names *Myiotheretes* and *Muscisaxicola*, and especially between the specific epithets *rufiventris* and *rufivertex*, are potential sources of ambiguity in the labeling of specimens of these related ground-tyrants. Thus, it seems likely that the labeling of SBMNH 166-25 as “*Muscisaxicola*



Fig. 3. A, Adult *Neoxolmis rufiventris* in open grass-shrub steppe near the Río Coig (Coyle) at site 77, southern Santa Cruz, Argentina (fig. 1; appendix 2). B, Same individual incubating.



Fig. 3. *Continued.* C, Same nest with clutch of 3 eggs. D, Close-up of same nest and eggs. See Maclean (1969, 1972, 1974). Photographs courtesy of G. L. Maclean, taken 4 December 1967.

rufivertex" is simply a product of clerical error.

Pemberton's five sets of eggs of *Neoxolmis rufiventris* were collected at ca. 775–1600 m elevation during the austral spring and summer, from 1 November–31 December 1911 (appendixes 2–3; fig. 1). WFVZ 15164 and 15166 were found at "Huana Luan," which corresponds to Estancia Huanu-Luan (fig. 1, 71 and 73) 88 km west-southwest of Maquinchao (Paynter, 1995: 327), at an elevation of ca. 950 m (Peters, 1923: 278); WFVZ 15165 was collected at 1600 m near Cerro Añecón (or Anecón) Grande (fig. 1, 72), a 1976 m peak 90 km east-southeast of San Carlos de Bariloche (Ejército Argentino, 1984; Paynter, 1995: 29); and SBMNH 166-25 and WFVZ 15167 were taken along the Arroyo Añecón (or Anecón) Grande (fig. 1, 74–75), which descends the northern slope of Cerro Añecón Grande to join the Arroyo Comallo at an elevation of ca. 775 m (Ejército Argentino, 1983, 1984; Paynter, 1995: 29). As noted by Peters (1923: 279), "The rainfall in the Huanuluan [sic]-Maquinchao region, as in other parts of Patagonia, is under ten inches [(25.4 cm)] annually, being precipitated mostly during the autumn and winter months. There are no trees and the scanty shrubs are of the general type found in arid regions . . . The bushes grow larger on the easterly slopes of the hills, which form a lee to the strong westerly winds so continuous in this part of the world." According to Pemberton (MS), *N. rufiventris* "frequents the level plateaus, mesas and plains which are covered with a low growth of brush and plenty of grass." All five of Pemberton's localities are situated in Patagonian steppe and semidesert (fig. 1, 71–75).

ADDITIONAL RECORDS: Santa Cruz: Kiff and Hough (1985: 106) report the presence of a set of eggs of "*Myiotheretes striaticollis*" in the Delaware Museum of Natural History that we would ascribe instead to *Neoxolmis rufiventris*. This clutch of two eggs, DMNH 23722 (fig. 4), was collected by A. T. Waldron on 25 October 1933 in "open camp" at "Estancia Condor, Rio Gallegos" (appendix 3). Estancia Condor (= "Ea. El Cóndor," Ejército Argentino, 1948a; cf. Paynter, 1995: 228–229, who notes that several ranches bear the name "El Cóndor" in Santa Cruz), a 200,000 ha sheep station in Patagonian steppe and semidesert at ca. 100



Fig. 4. DMNH 23722, clutch of 2 eggs of *Neoxolmis rufiventris* collected by A. T. Waldron in 1933 at site 76, southern Santa Cruz, Argentina (fig. 1; appendix 2). Each scale division = 1 cm. Photograph by D. Finnin, American Museum of Natural History.

m elevation in southeastern Santa Cruz, Argentina (fig. 1, 76), is situated ca. 16–64 km south of Río Gallegos, and it shares ca. 64 km of boundary fence with Chile, this border having been agreed to in 1903 as the result of a commission sent out by Edward VII at the request of Chile and Argentina. Estancia Condor was purchased by the Waldron family and others in 1880 when it was virgin land, and it was sold to the Menendez-Behety family in the mid-1960s (A. T. Waldron, personal commun.; Charles Bingham, personal commun.). It is presently owned by the Italian wool conglomerate Benetton (Allolio, 1996). A. T. Waldron (1990: 46) describes the climate of Estancia Condor as "dry"

with an annual rainfall of "12 inches" (30.48 cm).

The collector of DMNH 23722, Arthur Trengrouse Waldron (b. 13 May 1905, Berkshire, England), lived and worked at Estancia Condor or on an adjacent, family-owned *estancia* from 1924, when he first went out to Patagonia as a "jacaroo," or "cadet," to learn the management of sheep stations, until the mid-1960s, having become general manager of this and several other *estancias* in 1931 (A. T. Waldron, personal commun.; Charles Bingham, personal commun.). In addition to DMNH 23722 and a possible second set of eggs of *Neoxolmis rufiventris*, which he may have "sent to a friend, possibly in the north of the Argentine or in the [United] States" (Charles Bingham, personal commun.), but which we have been unable to trace, Waldron is known to have collected a skin of a Magellanic Plover, *Pluvianellus socialis*, and, in the 1920s, a small series of Patagonian birds' eggs, which he presented to the British Museum (now The Natural History Museum) in Kensington (A. T. Waldron, personal commun.) and to The Natural History Museum in Tring, England, respectively (Michael P. Walters, personal commun.).

By his own account, A. T. Waldron (personal commun.) "was and still . . . [is] very keen on birds and collected eggs in Patagonia purely as a hobby and . . . [has] long ago given them all away. The chocolate tyrant is or was a lovely bird and it was only rarely you would put one off its nest when riding round those vast areas with camps up to 10,000 acres [(4047 ha)]. These birds were not common but I fear nowadays they may suffer when they go north in winter from the trigger happy people."

The set slip of DMNH 23722 was labeled originally by Waldron as "*Myiotheretes rufiventris* Chocolate tyrant" before being re-labeled by another, unknown hand as "*Myiotheretes striaticollis*." *Myiotheretes striaticollis*, the Streak-throated Bush-Tyrant, an Andean tyrannid that ranges south to Tucumán and Catamarca, Argentina (Ridgely and Tudor, 1994), is not known to occur in Santa Cruz, whereas "*Myiotheretes*" (= *Neoxolmis*) *rufiventris* definitely breeds in the latter province during the austral spring.

Notes by Waldron on the set slip (appendix 3) concerning nest site ("In the open camp under a tuft of grass"), nest ("Lined with grass & feathers"), relative abundance and density ("Fairly common but never seen here more than a pair together"), appearance and behavior ("A very pretty bird with a flight somewhat resembling a thrush"), and vocalizations ("Have never heard them make any sort of call") are all strongly suggestive of *N. rufiventris*, and later recollections by Waldron (quoted above) are also evocative of this species. The egg specimens themselves closely match other, unambiguously identified sets of eggs of *N. rufiventris* as regards size (table 2), shape and coloration (fig. 4), to judge from available illustrations and descriptions of the sets collected by Pemberton (MS), Maclean (1969, 1972, 1974), and de la Peña (1985, 1987, 1988). Thus, we conclude that DMNH 23722 pertains to *N. rufiventris*, not *M. striaticollis*. The nest and eggs of *M. striaticollis* have not, to our knowledge, been described or reported in the literature.

GENERALIZATIONS: Pemberton's and Waldron's six nests of *Neoxolmis rufiventris* together triple the known sample of nesting sites for this species, which previously consisted of three published records (Maclean, 1969, 1972, 1974; de la Peña, 1985, 1987, 1988; Vuilleumier, 1994). At ca. 775–1600 m, the six known sites in Río Negro are geographically and altitudinally disjunct from the three known sites in Santa Cruz, which lie at or below 100 m. It remains to be seen whether further research will demonstrate that *N. rufiventris* breeds in intervening areas of Chubut and in those parts of Santa Cruz and Magallanes where we encountered the species, mostly as solitary individuals, during the austral spring of 1993 (fig. 1). As pointed out by Vuilleumier (1994: 21, 29, fig. 16), these apparent gaps in the breeding distribution of the Chocolate-vented Tyrant may be due to a lack of sampling, and there is no obvious biogeographical reason why these so-called "populations" should be disjunct.³

³ Similar apparent disjunctions in the breeding ranges of other Patagonian birds, for example *Muscisaxicola capistrata* (Vuilleumier, 1994: 36, fig. 22) and the Austral Canastero *Asthenes anthoides* (Furnariidae; Vuilleumier, 1997: 797–800), may likewise be attributable to inadequate sampling.

All 70 of our austral spring sightings of *Neoxolmis rufiventris* (fig. 1, 1–70), and all but one of the nine known spring and summer nests (fig. 1, 71–78), were situated within the region of Patagonian steppes and semideserts (Hueck and Seibert, 1981). The single apparent exception, Vuilleumier's (1994) site in south central Río Negro (fig. 1, 79), was located within the Monte of phytogeographers (Hueck and Seibert, 1981) but, in terms of its physiography and "steppe" vegetation, it is scarcely distinguishable from true Patagonian steppes. Thus, it seems reasonable to conclude that *N. rufiventris* breeds almost exclusively in Patagonian steppes and semideserts.

All nine nests of *Neoxolmis rufiventris* were placed in relatively sheltered locations, either at the base of one or more grass tussocks (WVZ 15165–15166, SBMNH 166-25, DMNH 23722; Vuilleumier, 1994; de la Peña, 1987), beside a small *Berberis buxifolia* shrub (Maclean, 1969), behind a rock (WVZ 15164), or inside a rock crevice (WVZ 15167). In eight out of nine cases (89%), *N. rufiventris* was found to be a ground-nester. In one case (WVZ 15167), representing an addition to the range of known nest sites, Pemberton discovered a nest 2.4 m up inside a vertical rock wall. In four other instances, he or his collectors discovered nests in more or less elevated positions on high plateaus (WVZ 15164, SBMNH 166-25) and on hillslopes (WVZ 15165–15166). Although nests of *N. rufiventris* have been reported on flat (Vuilleumier, 1994) and sloping ground (Maclean, 1969, 1972), Pemberton's observations indicate that this species is more catholic in its choice of nest sites than previously suspected. Nest sites in the Chocolate-vented Tyrant appear to span a topographic continuum, ranging from flat plains or plateaus to hillslopes and vertical escarpments.

Of the nine known nests of *Neoxolmis rufiventris*, eight (89%) were constructed mainly of grasses, which tend to predominate in Patagonian steppe biotopes, and all eight of these nests were placed on the ground surface. By contrast, the one known elevated rock crevice nest (WVZ 15167) was built mostly of sticks, straw, and wool. A platform of sticks (Maclean, 1969: 145, fig. 1) or

coarse grass stems (Vuilleumier, 1994: 31, fig. 17) was constructed adjacent to the nest cup in two instances, much as in *N. rubetra* (Vuilleumier, 1994: 25, fig. 14), in the former case "built up on the lower side of the slope [of an *arroyo*] so that the rim of the cup was level" (Maclean, loc. cit.; fig. 3, B, C, D). Three nest cups measured ca. 10–10.4 cm (mean: 10.1 cm) in diameter and ca. 4–6.9 cm (mean: 5.3 cm) in depth (Maclean, 1969: 145; de la Peña, 1985: 13, 1987: 154–155; Vuilleumier, 1994: 18). Feather linings, identified by Pemberton as "ostrich [= *Pterocnemia* (Rheidae)]" feathers in three nests (WVZ 15164–15166; appendix 3), and eggs or eggs plus young were found in eight of nine nests, the only exception being Vuilleumier's (1994) nest, which lacked a feather lining and contained two young but no eggs. This pattern suggests that the feather lining may be dispensed with once the entire clutch has hatched. A solitary, incubating or brooding parent was flushed from each of three nests (WVZ 15165, SBMNH 166-25; Maclean, 1969). Near another nest watched by Vuilleumier (1994), two parent birds emitted alarm calls in the vicinity of their two large downy young, thus indicating that care of the brood may be biparental.

Eight clutches ranged from 1–3, and averaged 2.0 eggs (table 2). Fourteen eggs averaged 30.08×21.24 mm, and were ovoidal with very pale pink or cream ground color and sparse reddish and pale gray spots near the larger pole (figs. 3–4; Pemberton, MS; Maclean, 1969, 1972, 1974; de la Peña, 1985, 1987, 1988; personal obs.). Dates for these eight clutches ranged from 25 October–31 December (appendixes 2–3); individual clutches ranged from fresh (7 November, 3–4 and 23 December), half-incubated (1 November), or pipped (9–10 November), to added (31 December). Nestlings were found in two nests on 7 November, in Río Negro (Vuilleumier, 1994) and Santa Cruz (MRDLP 379) respectively. Egg and nestling dates together indicate that the breeding season extends from ca. late October–late December and partly coincides in Río Negro (1 November–23 December) and Santa Cruz (25 October–4 December). In Río Negro, breeding may take place later at relatively high, 1600 m elevations (9 November–23 December) than at lower, 775–1100 m el-

evations (1–10 November; Pemberton, MS). Partial coincidence of breeding phenology between the Río Negro and Santa Cruz populations, presence of suitable breeding (steppe) habitat in intervening parts of Chubut, and probable commingling of migrants from Río Negro and Santa Cruz on wintering grounds in northern Argentina, Uruguay, and southeastern Brazil, suggest the possibility of gene flow between the northern and southern breeding populations of *Neoxolmis rufiventris*.

COMPARATIVE BREEDING BIOLOGY

SYSTEMATIC POSITION OF *NEOXOLMIS RUFIVENTRIS*: The Chocolate-vented Tyrant has occupied a more or less isolated taxonomic position within the Tyrannidae for over half a century (Vuilleumier, 1994: 16), ever since Hellmayr (1927: 39, footnote b) transferred *rufiventris* from *Myiotheretes* to a new monotypic genus *Neoxolmis*. Traylor (1977: 163) expanded *Neoxolmis* to include the Rusty-backed Monjita *N. rubetra*, which had traditionally been placed in *Taenioptera* (Sclater, 1888: 16) or *Xolmis* (Hellmayr, 1927: 18). Lanyon (1986: 46–47) concurred with Traylor's (1977) placement of *rubetra* with *rufiventris* in *Neoxolmis*, and he expressed doubt that the terrestrial *rufiventris* and the more arboreal *rubetra*, which differ greatly in external morphology, could be differentiated at the generic level on the basis of syringeal structure (Lanyon, 1986: 50–51). Lanyon's concept of *Neoxolmis* left out of account the Salinas Monjita *N. salinarum*, which Nores and Yzurieta (1979: 7–8) described as a new subspecies of *Xolmis rubetra*, and which various authors have either elevated to the level of a full species in *Xolmis* (Olrog, 1984: 260; Ridgely and Tudor, 1994: 609–610) or *Neoxolmis* (Narosky and Yzurieta, 1989: 210), or retained as a subspecies of *N. rubetra* (Fjeldså and Krabbe, 1990: 503).

Lanyon (1986: 42–53) employed 25 plumage, syringeal, and osteological characters in an analysis of the phylogenetic relationships of *Neoxolmis* to other genera of the bush and ground tyrant assemblage, termed by him the *Muscisaxicola* group (our fig. 5), whose monophyly had “traditionally . . . been based on shared ecological and behavioral traits, the morphological correlates of a terrestrial

way of life, and biogeographical considerations” (Lanyon, 1986: 42). His study demonstrated a sister-group relationship between *Neoxolmis* and a clade comprising the monotypic *Gubernetes* and *Muscipipra*, based on the presence, in the syringes of all three genera, of very broad and J-shaped internal cartilages (Lanyon, 1986: 50–51; our fig. 5, 3). Although Lanyon (1986) summarized information on eggs, nests, and nest sites within the *Muscisaxicola* group, he refrained from utilizing these aspects of reproductive biology in his phylogenetic analysis. Similarly, Smith (1971: 242), Vuilleumier (1971, 1994: 37–39), and Traylor and Fitzpatrick (1982: 14–16, 22–23) surveyed nest form and nest site variability in bush and ground tyrants, but found these data to be, for the most part, phylogenetically uninformative.

Nest form is considered “one of the more conservative features of flycatcher biology” (Traylor and Fitzpatrick, 1982: 14), and it has traditionally been accorded considerable weight in tyrannid classification (Ihering, 1904; Lanyon, 1985; Sick, 1993: 455–457). As noted by Ihering (1904: 315) and Traylor and Fitzpatrick (loc. cit.), the most common, and probably primitive, nest form is the open cup, exemplified by the ground-surface nest of *Neoxolmis rufiventris* (Traylor and Fitzpatrick, 1982: 15, fig. 3c). Open-cup nests are ubiquitous in the *Muscisaxicola* group, being present in all of the approximately eight genera and 28 species in which the nest is known (table 3). Hole-nests, such as the obligatory tree-cavity nests that comprise a shared derived character of the myiarchine flycatchers, and the facultative tree-cavity nests of unrelated *Xolmis* species, are relatively uncommon (Lanyon, 1985; Sick, 1993: 457). Other uncommon nest forms include covered nests, which appear to be derived from the open cup, and pendant, pyriform nests, which are considered the most elaborate and derived nests (Weyrauch, 1941: 359–360; Traylor and Fitzpatrick, 1982: 16). Oology has also been accorded much weight in tyrannid systematics, for example in the delimitation of some genera and subfamilies on the basis of egg form and coloration (Ihering, 1904; Schönwetter and Meise, 1979; Sick, 1993: 458).

Nest form is subject to convergence

(Koepcke, 1972), and other reproductive variables, such as clutch size, may not be strongly constrained by phylogeny (Murphy, 1989). Hole-nests are widely interpreted as products of natural selection that resist predation (*Resistenzformen*; Koepcke, 1972), nest parasitism, and climatic extremes, and thereby enhance reproductive success (Dorst, 1962; Lack, 1968; Verbeek, 1981). However, relative breeding success of hole-nesting and open-nesting species may not differ significantly, and opposing selection pressures on hole- and open-nesting birds may be in balance (Nilsson, 1986).

In the present section, we briefly analyze variation in nest site and clutch size in *Neoxolmis rufiventris* and other members of the *Muscisaxicola* group of tyrannids (sensu Lanyon, 1986), based on a partial survey of the literature, in an attempt to place the above documented surface- and crevice-nesting habits of the Chocolate-vented Tyrant in phylogenetic and evolutionary contexts, and to extend the preliminary surveys of nest site variability in bush and ground tyrants by Smith (1971), Vuilleumier (1971, 1994), Traylor and Fitzpatrick (1982), and Lanyon (1986).

THE MUSCISAXICOLA GROUP: Vuilleumier (1971) and Smith (1971) interpreted the bush tyrants (*Xolmis*, *Pyrope*, *Myiotheretes*, and *Ochthoeca*) and ground tyrants (*Agriornis*, *Neoxolmis*, *Muscisaxicola*, and *Muscigralla*) of the high Andes, Patagonia, and south-central Brazil as a more or less closely interrelated, monophyletic group of tyrannids, and Vuilleumier (1971: 164) postulated a major ecological shift during the evolutionary history of the bush and ground tyrants, "both from arboreal to terrestrial habits and from a relatively closed habitat (woodland) to a much more open one (steppe)." Fitzpatrick (1985: 463–464) identified a major pathway of trophic specialization within the bush and ground tyrant assemblage, with arboreal foliage-gleaners (e.g., *Ochthoeca*) having given rise to facultative perch-to-ground predators (e.g., *Xolmis*), which in turn gave rise to derived ground feeders (e.g., *Neoxolmis*, *Muscisaxicola*, *Muscigralla*). Keast (1972: 264) suggested that the ground feeders (e.g., *Muscisaxicola*, *Muscigralla*) may have excluded similar, chatlike turdids from South America through competition.

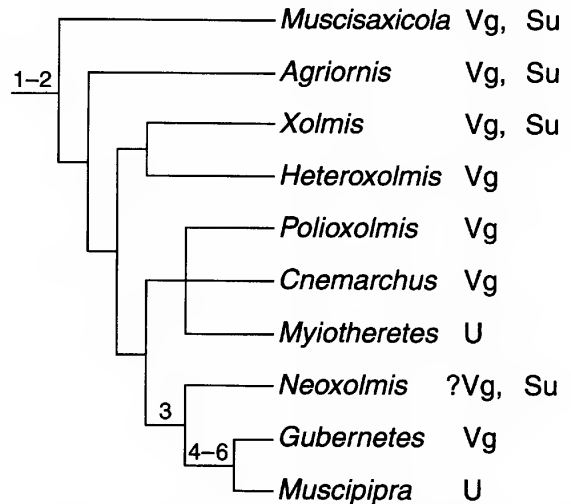


Fig. 5. Phylogenetic relationships and possible convergent evolution of terrestrial nesting within the *Muscisaxicola* group (partly after Lanyon, 1986: 43–44). Note the widespread taxonomic distribution and apparent plesiomorphy of raised open-cup nests in vegetation (Vg). Clade geometry, derived from nonreproductive characters including those listed here (1–6), suggests that surficial or subterranean cup nests (Su) and relatively small, 2-egg clutches (tables 3–4) evolved convergently in Andean *Muscisaxicola* and cis-Andean *Neoxolmis*, and possibly also in some *Agriornis* and *Xolmis* spp. Characters: 1, Internal cartilages of syrinx broad and robust (all taxa in group except *Cnemarchus*); 2, Outer web of outer rectrix pale (all taxa except *Heteroxolmis*); 3, Internal cartilages of syrinx very broad and J-shaped (*Neoxolmis*, *Gubernetes*, and *Muscipipra*); 4, Tail elongated and forked (*Gubernetes* and *Muscipipra*); 5, Dorsal end of B1 element of syrinx bulbous (idem); 6, Ventral end of B2 element of syrinx forked (idem). U, Nest unknown. Nest data from table 3.

The *Muscisaxicola* group (table 3, fig. 5) presently consists of 34 species in the genera *Muscisaxicola* (12 species), *Agriornis* (5), *Xolmis* (including *Pyrope*; 5), *Heteroxolmis* (a new genus for *dominicana*; 1), *Polioxolmis* (a new genus for *rufipennis*; 1), *Cnemarchus* (1), *Myiotheretes* (4), *Neoxolmis* (3), *Gubernetes* (1), and *Muscipipra* (1), and it excludes *Ochthoeca* and *Muscigralla*. Of the 10 included genera, all except *Cnemarchus* are said to possess broad and robust internal cartilages of the syrinx (fig. 5, 1), and all except *Heteroxolmis* possess a pale outer

web of the outer rectrix (fig. 5, 2); Lanyon (1986: 44, table 5) interprets both of these characters as synapomorphies for the *Muscisaxicola* group. Within this group, genera are clustered on the basis of other derived characters of the plumage and, to a lesser extent, of the syrinx and nasal capsule. *Muscisaxicola* is considered to be more distantly related to the other nine genera than the latter are to each other, and *Agriornis* is interpreted as the sister group of the remaining eight genera. *Polioxolmis*, *Cnemarchus*, and *Myiotheretes* comprise an unresolved trichotomy that is the sister group of *Neoxolmis* and its sister group *Gubernetes* plus *Muscipipra*. These six genera are interpreted as the sister group of *Xolmis* plus *Heteroxolmis*.

Of the 10 genera included by Lanyon (1986) in his *Muscisaxicola* group, data on nesting behavior are, as far as we are aware, largely or entirely lacking for two (Schönwetter and Meise, 1979: 841): *Myiotheretes* (comprising four species, *striaticollis*, *pernix*, *fumigatus*, and *fuscorufus*) and *Muscipipra* (comprising one species, *vetula*). The eggs of *Muscisaxicola frontalis*, *Agriornis andicola*, and *Cnemarchus erythropygius*, and the nest and eggs of *Neoxolmis* (or *Xolmis*) *salinarum*, are likewise apparently undescribed (Schönwetter and Meise, loc. cit.; personal obs.), although Navas and Bó (1994: 92) briefly mention an egg of *Muscisaxicola frontalis*. Prior to the recent descriptions of the nest site, nest, and eggs of *Heteroxolmis dominicana* by Fontana (1994, 1997), knowledge of breeding of this rare and vulnerable species (Collar et al., 1994: 141) was limited to reports of habitat requirements (Oriens, 1978), nesting (Gerzenstein, 1967: 457), and isolated eggs (Nehrkorn, 1899: 136, 1910: 161; Ihering, 1900: 224, identification questionable according to Fontana, 1997: 81; Schönwetter and Meise, 1979: 71, 88; de la Peña, 1988: 60).

NEST SITE AND CLUTCH SIZE VARIATION: Table 3 summarizes nest site and clutch size variation in *Muscisaxicola*, *Agriornis*, *Xolmis*, *Heteroxolmis*, *Polioxolmis*, *Cnemarchus*, *Neoxolmis*, and *Gubernetes*, with the exception of the aforementioned poorly known species. Nest sites are classified according to the following typology: open nests in trees or bushes (To); hole- or crevice-nests

in trees or posts (Th), including tree-cavities formerly occupied by Picidae (Belton, 1985: 56); disused, covered nests of Furnariidae or Psittacidae in trees or other sites (Tf); nests in grass or sedge clumps (G); ground-surface nests (S); crevice-nests (C); and burrows (B), including former picid burrows in terrestrial termite nests (Sick, 1993: 457) and burrows in anthills (Ihering, 1914: 438, 477–478). Clutch size is reported for each genus as a range that includes both observed clutch sizes and estimates derived from brood sizes.

Open-cup tree or shrub nests (To), which are considered relatively primitive in structure (Traylor and Fitzpatrick, 1982: 14; Collias, 1997: 258), have been confirmed for all of the aforementioned genera except *Neoxolmis* and *Gubernetes*. The widespread distribution of this nest type thus supports its inferred plesiomorphy. Tree-hole and tree-crevice (Th) and furnariid and psittacid nest (Tf) occupation are restricted to *Xolmis* species. *Xolmis* is the most catholic genus as regards nest site preferences, which include all sites except surficial ones (S), and, perhaps in part as a result of its versatility, it has the largest reported clutch (5) of any member of the *Muscisaxicola* group. Grass or sedge clump-nesting (G) has only been reported in one of five species of *Agriornis*, in one of five species of *Xolmis*, and in the monotypic *Heteroxolmis* and *Gubernetes*. Surface-nesting (S) occurs in two of 12 species of *Muscisaxicola*, in one of five species of *Agriornis*, and in both *Neoxolmis rubetra* and *N. rufiventris*. This mode of nesting is therefore characteristic of *Neoxolmis*, but is rather atypical of *Muscisaxicola* and *Agriornis*. Crevice-nesting (C) is found in 10 of 12 species of *Muscisaxicola*, which is a quintessential crevice-nester, and in two of five species of *Agriornis*, one of five species of *Xolmis*, and one of two species of *Neoxolmis* for which data are available. Burrow-nesting (B) occurs in two of 12 species of *Muscisaxicola* and in three of five species of *Xolmis*. Clutch-size ranges of genera show few obvious correlations with nest site. However, it is noteworthy that crevice nests of high Andean *Muscisaxicola* species have a modal clutch size of 2, whereas *M. fluviatilis*, the only ground-tyrant in the Amazon lowlands,

TABLE 3
Species Diversity, Nest Site Variation, and Clutch Size in the *Muscisaxicola* Group^a

Genus	N	Number of species per nest type							Clutch size	Source
		To	Th	Tf	G	S	C	B		
<i>Muscisaxicola</i>	12	1	—	—	—	2	10	2	2–4	1
<i>Agriornis</i>	5	4	—	—	1	1	2	—	1–4	2
<i>Xolmis</i>	5	3	3	4	1	—	1	3	1–5	3
<i>Heteroxolmis</i>	1	1	—	—	1	—	—	—	2–4	4
<i>Polioxolmis</i>	1	1	—	—	—	—	—	—	2	5
<i>Cnemarchus</i>	1	1	—	—	—	—	—	—	—	6
<i>Myiotheretes</i>	4	—	—	—	—	—	—	—	—	—
<i>Neoxolmis</i>	3	1?	—	—	—	2	1	—	1–3	7
<i>Gubernetes</i>	1	—	—	—	1	—	—	—	3	8
<i>Muscipipra</i>	1	—	—	—	—	—	—	—	—	—

^aNumber of species per genus or nest type, and number of eggs per genus including observed clutch sizes (c) and estimates derived from brood sizes (b). Additional symbols are: N, Number of species per genus; To, open nest in tree or shrub; Th, hole- or crevice-nest in tree or post; Tf, disused furnariid or psittacid nest, typically in tree; G, grass or sedge clump nest; S, ground-surface nest; C, crevice- or hole-nest in rock or manmade structure; B, burrow-nest; *, source used to compile frequency distribution and mean of clutch size or brood size in table 4.

Note—Sources of data are as follows:

1—To: *Muscisaxicola fluvialis*: Sclater and Salvin (1873: 277–278). S: *M. maculirostris*: Johnson (1967: 249), de la Peña (1988: 66); *M. macloviana*: Pässler (1922: 466). C: *M. macloviana*: Woods (1970: 22, 23; 1988: 216), Canevari et al. (1991: 357), Strange (1992: 97); *M. capistrata*: Johnson (1967: 252), de la Peña (1988: 65), Vuilleumier (1994: 28, 35, 38), Andors and Vuilleumier (personal obs., nest in crevice of lava flow with 2 volant young respectively inside and in vicinity, Reserva Natural Provincial “Laguna Azul,” Santa Cruz, Argentina, 23 November 1993); *M. rufivertex*: Barros (1945: 185), Salvador and Narosky (1984: 134–135), Salvador and Salvador (1984: 124; 1988: 21), de la Peña (1988: 63), Canevari et al. (1991: 354); *M. juninensis*: Johnson (1967: 243, determination tentative), de la Peña (1988: 64); *M. albilora*: Barros (1945: 185), Philippi et al. (1954: 48), de la Peña (1988: 63), Canevari et al. (1991: 355); *M. alpina*: Venero and Brokaw (1980: 23), de la Peña (1988: 65), Venero (1990: 3, 5), Canevari et al. (1991: 356); *M. cinerea*: Barros (1945: 185), Johnson (1967: 244), Hoy (1980); *M. albifrons*: Johnson (1967: 247, determination tentative); *M. flavinucha*: Barros (1945: 185), Johnson (1967: 238), de la Peña (1988: 64), Canevari et al. (1991: 355), Vuilleumier (personal obs., open cup nest on ground, well hidden under volcanic rocks, 2 young, ca. 1420 m, Volcán Llaima, Chile, 27 February and 2 March 1965; 1994: 37); *M. frontalis*: Johnson (1967: 246), de la Peña (1988: 65), Canevari et al. (1991: 356). B: *M. capistrata*: Philippi et al. (1954: 48–49), Smith (1971: 242), Fjeldsø and Krabbe (1990: 510), Canevari et al. (1991: 356), Ridgely and Tudor (1994: 606); *M. rufivertex*: Dorst (1962: 11–13). c, b: *M. maculirostris* (c/2–3): Johnson (1967: 249), de la Peña (1988: 66); *M. fluvialis* (c/4): Sclater and Salvin (1873: 278); *M. macloviana* (c/2–3): Pässler (*1922: 466), de la Peña (1988: 66), Woods (1988: 216); *M. capistrata* (c/2–3, b/2–3): Philippi et al. (*1954: 49), Johnson (1967: 252), de la Peña (1988: 65), Canevari et al. (*1991: 356), Vuilleumier (1994: 28), Andors and Vuilleumier (*personal obs.; see C); *M. rufivertex* (c/2–3, b/2–3): Dorst (*1962: 13–14), Salvador and Narosky (*1984: 134–135), Salvador and Salvador (*1984: 124; *1988: 21), Canevari et al. (1991: 355); *M. juninensis* (c/2–3): Johnson (*1967: 243, determination tentative), de la Peña (*1988: 64); *M. albilora* (c/2–3): de la Peña (*1988: 63), Canevari et al. (1991: 355); *M. alpina* (c/2–4): Venero and Brokaw (*1980: 23), de la Peña (1988: 65), Venero (1990: 6), Canevari et al. (*1991: 356); *M. cinerea* (c/2): Hoy (*1980); *M. albifrons* (c/2): Johnson (*1967: 247–248, determination tentative); *M. flavinucha* (c/2–4, b/2): Johnson (1967: 238), de la Peña (*1988: 64), Canevari et al. (1991: 355), Vuilleumier (*personal obs.; see C); *M. frontalis* (b/2): Johnson (*1967: 246).

2—To: *Agriornis montana*: Vuilleumier (1994: 39); *A. livida*: Barros (1945: 193), Johnson (1967: 226); *A. microptera*: Peters (1923: 319), Johnson (1967: 232, determination tentative), de la Peña (1989), Canevari et al. (1991: 349), Casas (1992: 251); *A. murina*: Nores and Salvador (1990: 161), Andors and Vuilleumier (1996: 111–113, 115). G: *A. microptera*: de la Peña (1977: 148). S: *A. andicola*: Vuilleumier (1994: 24, 26, 33, 39). C: *A. montana*: Taczanowski (1874: 532), Barros (1945: 193), Johnson (1967: 229, 231), Hoy (1976: 205), Venero and Brokaw (1980: 22), Narosky et al. (1984: 210), Salvador and Salvador (1988: 21), Canevari et al. (1991: 350), Vuilleumier (1994: 39); *A. livida*: Germain (1860: 311), Barros (1945: 193). c, b: *A. montana* (c/2–4): Taczanowski (*1874: 532), Johnson (*1967: 229–231), Hoy (*1976: 205, 207), Venero and Brokaw (*1980: 22), de la Peña (1988: 58), Canevari et al. (1991: 350); *A. andicola* (b/2): Vuilleumier (*1994: 26, 34); *A. livida* (c/2–4): Germain (1860: 311), Johnson (1967: 226), de la Peña (1988: 57), Canevari et al. (1991: 349); *A. microptera* (c/1–3): Peters (*1923: 319), Johnson (*1967: 232, determination tentative), de la Peña (*1977: 148; 1988: 57; *1989), Canevari et al. (*1991: 349), Casas (*1992: 251); *A. murina* (c/3): Nores and Salvador (*1990: 161), Andors and Vuilleumier (*1996: 113, 115).

TABLE 3
Continued

- 3-To: *Xolmis pyrope*: Germain (1860: 311), Pässler (1922: 463–464), Barros (1945: 190), Johnson (1967: 265), Vuilleumier (1994: 10–11, 17, 38); *X. cinerea*: Dalglish (1881: 243), Aplin (1894: 175–176), Ihering (1900: 223), Hartert and Venturi (1909: 189), Hudson (1920: 141), Belton (1985: 53); *X. coronata*: Hudson (1920: 142). Th: *X. cinerea*: de la Peña (1985: 13–14; 1987: 155–156; 1988: 60), Canevari et al. (1991: 351); *X. velata*: Dubs (1983: 88; 1992: 99); *X. irupero*: Dalglish (1881: 244), Barrows (1883: 139), Hudson (1920: 146), Wetmore (1926a: 300), Mogensen (1930: 294), Belton (1985: 56), de la Peña (1977: 150; 1985: 14; 1987: 156–157; 1988: 61), Canevari et al. (1991: 352), Dubs (1992: 99), Sick (1993: 457), Ridgely and Tudor (1994: 609). Tf: *X. cinerea*: Sick (1993: 429, 456); *X. coronata*: Contino (1982: 86), de la Peña (1977: 149; 1988: 61); *X. velata*: Sick (1993: 429, 457); *X. irupero*: Dalglish (1881: 244), Aplin (1894: 177), Ihering (1900: 223; 1914: 438, 477–478), Hartert and Venturi (1909: 190), Hudson (1920: 146), Contino (1982: 87), Belton (1985: 56), Martella et al. (1985: 49, 50), de la Peña (1977: 150; 1985: 14; 1987: 156–157; 1988: 61), Canevari et al. (1991: 352), Sick (1993: 457). G: *X. coronata*: Hudson (1920: 142). C: *X. pyrope*: Germain (1860: 311), Canevari et al. (1991: 354). B: *X. cinerea*: Hudson (1920: 141); *X. velata*: Sick (1993: 457); *X. irupero*: Ihering (1914: 438, 477–478). c, b: *X. pyrope* (c/2–4): Germain (1860: 311), Pässler (1922: 463), Johnson (1967: 265), de la Peña (1988: 62); *X. cinerea* (c/1–5): Dalglish (*1881: 243), Aplin (*1894: 175–176), Euler (1900: 38), Hartert and Venturi (*1909: 189), Chubb (1910: 572), Hudson (*1920: 141), Smyth (1928: 134), Belton (*1985: 53), de la Peña (1977: 148; *1985: 13–14; *1987: 155–156; 1988: 60), Canevari et al. (1991: 351); *X. coronata* (c/3–5): Hartert and Venturi (1909: 190), Hudson (*1920: 142–143), Contino (*1982: 86), de la Peña (*1977: 149; *1988: 61); *X. velata* (c/2): Gene K. Hess (personal commun., DMNH 23696, 2-egg clutch collected by Clement Gordon McEwen, Concepción, Ñuflo de Chávez, Santa Cruz, Bolivia, 7 February 1923); *X. irupero* (c/2–5, b/1–3): Dalglish (*1881: 244), Hartert and Venturi (1909: 190), Hudson (*1920: 146–147), Wetmore (*1926a: 300), Smyth (1928: 134), Mogensen (*1930: 294), Pergolani de Costa (1949: 14), Contino (*1982: 87), de la Peña (1977: 150; 1983: 166; *1985: 14, 5 clutches including 2 eggs + 1 nestling counted as 3-egg clutch; *1987: 156–157; 1988: 61), Martella et al. (*1985: 50), Canevari et al. (1991: 352).
- 4-To: *Heteroxolmis dominicana*: W. Belton in Fontana (1994: 36; 1997: 79). G: *H. dominicana*: Fontana (1994: 36–39; 1997: 80–81). c, b: *H. dominicana* (c/3–4, b/2–4): Fontana (*1994: 39, tabela 4; *1997: 80, table 1).
- 5-To: *Polioxolmis rufipennis*: Venero and Brokaw (1980: 22), Venero (1990: 2, 5), Fjeldså (1990: 27), Fjeldså and Krabbe (1990: 499), Vuilleumier (1994: 4–5, 9, 10, 13, 37). c, b: *P. rufipennis* (c/2, b/2): Venero and Brokaw (*1980: 22), Venero (*1990: 6), Fjeldså (*1990: 27), Vuilleumier (*1994: 5, 9).
- 6-To: *Cnemarchus erythropygius*: Fjeldså and Krabbe (1990: 499).
- 7-To: *Neoxolmis rubetra*: Vuilleumier (1994: 13–14, identification uncertain). S: *N. rubetra*: Vuilleumier (1994: 13–14, 25); *N. rufiventris*: Maclean (1969: 145; 1972: 1974: 190–191), de la Peña (1985: 13; 1987: 154–155, 245; 1988: 59), Canevari et al. (1991: 351), Vuilleumier (1994: 16, 18, 31), Andors and Vuilleumier (this paper). C: *N. rufiventris*: Andors and Vuilleumier (this paper). c, b: *N. rubetra* (c/?1, b/2): Vuilleumier (*1994: 13–14, 25); *N. rufiventris* (c/1–3, b/2): Maclean (*1969: 145; *1972; *1974: 190–191), Schönwetter and Meise (1979: 828), de la Peña (*1985: 13; *1987: 154–155, 245; *1988: 59, 2 eggs + 1 nestling counted as 3-egg clutch), Canevari et al. (1991: 351), Vuilleumier (*1994: 18, 31), Andors and Vuilleumier (*this paper).
- 8-G: *Gubernetes yetapa*: Chubb (1910: 574). c, b: *G. yetapa* (c/3): Chubb (*1910: 574), de la Peña (1988: 69).

reportedly nests in trees and has a clutch size of 4 (Sclater and Salvin, 1873: 277–278).

CLUTCH SIZE OR BROOD SIZE VERSUS NEST SITE: Table 4 analyzes the relationship between clutch size or brood size and nest type for a subset of the nest records used to compile the generalized clutch size ranges in table 3. Records lacking indications of frequency are for the most part omitted, as per the recommendation of Moreau (1944: 290), although some clutch or brood sizes of unknown frequency are included, and arbitrarily assigned a frequency of $N = 1$, if (a) they are accompanied by information on nest site, and (b) they are integral in value and not an explicit average or a range. Frequency distributions of

clutch size and brood size are given for each of seven nest types, and as sums for open (To, G, S) and hole (Th, Tf, C, B) nests, assuming functional equivalence of the nest types within each category.

Table 4 shows that, within the *Muscisaxicola* group, mean clutch size is least (2.3) in crevice (C) nests, greater (2.5–3.0) in surficial (S), open arboreal or shrub (To), borrowed furnariid and psittacid (Tf), and burrow (B) nests, and greatest (3.3–3.8) in grass or sedge clump (G) and tree-hole nests (Th). Modal clutch size follows a similar trend, being least (2–3) in C and S, intermediate (3) in To, Tf, G, and B, and greatest (4) in Th nests. The open- and hole-nest categories, when summed, yield

TABLE 4
Frequency Distributions and Means of Clutch Size and Brood Size, Grouped by Nest Type, in Samples of the *Muscisaxicola* Group^a

Nest type	Clutch size								Brood size							
	1	2	3	4	5	Mean	SD		0	1	2	3	4	5	Mean	SD
To	4	1	7	2	0	2.5	1.0919		0	0	3	0	0	0	2.0	0
G	0	0	4	2	0	3.3	0.5164		2	0	1	1	1	0	1.8	1.7889
S	0	4	4	0	0	2.5	0.5345		0	0	3	0	0	0	2.0	0
Open	4	5	15	4	0	2.7	0.9049		2	0	7	1	1	0	1.9	1.1362
Th	0	1	0	3	1	3.8	0.9832		0	1	0	1	0	0	2.0	1.4142
Tf	0	2	9	1	0	2.9	0.5149		0	0	0	1	0	0	3.0	0
C	1	9	3	1	0	2.3	0.7263		0	0	4	1	0	0	2.2	0.4472
B	0	0	1	0	0	3.0	0		0	0	1	0	0	0	2.0	0
Hole	1	12	13	5	1	2.8	0.8701		0	1	5	3	0	0	2.2	0.6667

^a Data shown are compiled from sources marked with asterisks (*) in table 3. Modal frequencies are italicized. For explanations of nest site symbols, see text and table 3. Additional symbols are: SD, standard deviation of sample; **Open**, sum of **To**, **G**, and **S**; **Hole**, sum of **Th**, **Tf**, **C**, and **B**.

(a) respective mean clutch sizes of 2.7 and 2.8, (b) respective mean brood sizes of 1.9 and 2.2, and (c) identical modal clutch sizes of 3. Results (a) and (c) are reminiscent of Nilsson's (1986) finding that, in samples of European open-nesting and hole-nesting bird species, breeding success is approximately the same. Results (a) and, especially, (b) are consistent with Lack's (1968) and Skutch's (1985) findings that, in mid-European and Neotropical passerines and in various anatids, clutch size is on average larger in roofed or hole-nests than in nests of the open-cup type.

The sample of hole-nesting taxa analyzed in tables 3 and 4 is dominated numerically by crevice-nesting *Muscisaxicola* species, the nest-holes of which are often little more than narrow rock crevices in relatively barren, high Andean environments where space and resource limitations may preclude the raising of large broods. Such crevice-nests afford protection from wind chill (Collias, 1997: 263), but have smaller modal clutches (2) than other types of hole-nests (3–4), which may be generally better sheltered and more capacious. Similarly, the modal clutch size of surface-nests (2–3), including the ground nest of steppe-inhabiting *Neoxolmis rufiventris*, tends to be smaller than that of other types of open-nests (3), which generally occur in more heavily vegetated and sheltered

environments where they are usually placed in bushes or trees. These trends suggest that clutch size in the *Muscisaxicola* group may be space- and resource-limited.

EVOLUTIONARY AND BIOGEOGRAPHIC PATTERNS: Lanyon's (1986: 43, fig. 24) hypothesis of phylogenetic relationships within the *Muscisaxicola* group was founded on non-reproductive characters, and nest and clutch characteristics may therefore be used to consider the evolutionary and biogeographic implications of his cladogram without risk of circularity. If the open-cup arboreal or shrub nest is indeed primitive for the *Muscisaxicola* group, as was suggested above, and if members of the bush and ground tyrant assemblage are correctly interpreted as having invaded open habitats and acquired obligatory ground-feeding adaptations relatively late in their evolutionary history (Vuilleumier, 1971; Fitzpatrick, 1985), then the ground-nesting habits of typical *Muscisaxicola* and *Neoxolmis*, and of some *Agriornis* and *Xolmis* species, may reasonably be interpreted as derived conditions. *Muscisaxicola* and *Neoxolmis* are but distantly related to each other within the *Muscisaxicola* group, and their terrestrial nesting habits and reduced clutch sizes may therefore have evolved independently. This conclusion is reinforced by the geometry of Lanyon's (1986) cladogram (our fig. 5), which implies that

tree- or shrub-nesting *Agriornis*, *Xolmis*, *Heteroxolmis*, *Polioxolmis*, and *Cnemarchus* species are more closely related to ground-nesting *Neoxolmis* than any of these taxa is to *Muscisaxicola*. Lanyon (1986: 44, table 5) interprets *Muscipipra*, for which the nest is unreported (Lanyon 1986: 52), and grass clump-nesting *Gubernetes* as sister taxa, based on possession of an elongated, forked tail and two syringeal synapomorphies (our fig. 5, 4–6), and he unites the *Muscipipra-Gubernetes* clade with ground-nesting *Neoxolmis* based on a third syringeal synapomorphy cited above (our fig. 5, 3). It remains to be seen whether the nest site preferences of *Muscipipra* will be found to resemble those of *Gubernetes* and *Neoxolmis*, whose semiterrestrial and terrestrial nesting habits may perhaps be an additional indication of close relationship.

The *Neoxolmis-Gubernetes-Muscipipra* clade inhabits cis-Andean lowlands (sensu Fjelds , 1992: 13, fig. 2C), whereas its sister group, the *Polioxolmis-Cnemarchus-Myiotheretes* trichotomy, is largely montane, and *Polioxolmis* and *Cnemarchus* in particular are more or less restricted to relict, high-altitude *Polylepis* (Rosaceae) or other woodlands, or to *Puya Raimondii* (Bromeliaceae) stands, of the Andes (Vuilleumier, 1969: 604–605, 1986: 605–607, 1994: 4–6, 8–11, 13, 15; Fjelds , 1990, 1991: 344, 1992: 21, 34, 60). Such monotypic and “ancient” *Polylepis* specialists as *Polioxolmis rufipennis*, which have their nearest sister taxa in humid montane forest or in cis-Andean lowlands (Fjelds , 1991: 347; 1992: 34, 60), and which may have differentiated in the late Pliocene (Fjelds , 1992: 34), were apparently isolated in elevated *Polylepis* woodlands by habitat contractions during periods of Pleistocene aridity or cold (Fjelds , 1992: 44). Entrapment (Vuilleumier, 1986: 606) of *Polioxolmis* and *Cnemarchus* in relictual *Polylepis* woodlands evidently permitted the retention of plesiomorphic arboreal and shrub breeding habits. In the cis-Andean rain shadow, on the other hand, selection apparently favored adoption of derived terrestrial nesting habits (with concomitantly reduced clutch sizes) in such taxa as *Neoxolmis* that successfully invaded, and adapted to, semiarid steppes.

Within *Agriornis*, the large high-Andean species *montana* and *andicola* both possess an extensively white tail, which may be a synapomorphy (Fjelds , 1991: 344; 1992: 60); both affect open arid areas, including *Poly-lepis* woodlands, where they occur either locally (*montana*) or as a rare and declining specialist of these and other woods (*andicola*; Fjelds , 1991: 344, 1992: 21; Collar et al., 1994: 141; Krabbe et al., 1996); and both nest terrestrially (table 3), though *montana* also nests in the giant bromeliad *Puya Raimondii* (Vuilleumier, 1994: 39), and *andicola* may likewise depend on *Puya* (Collar et al., loc. cit.; Vuilleumier, 1994: 24, 26–28, 32, 33). The large Andean and Patagonian species *livida* and *microptera*, and the small and apparently plesiomorphic Argentinian species *murina* (Fjelds , 1992: 60; Andors and Vuilleumier, 1996), nest arboreally or in bushes, and *livida* also nests in crevices, in semiarid scrublands (table 3). Ground-nesting in the *montana-andicola* clade is correlated with adaptation to relatively open (in this case, arid) habitats, whereas arboreal or shrub-nesting in other *Agriornis* species is associated with occupation of more closed (semiarid) environments. Other taxa in the *Muscisaxicola* group present similar biogeographic patterns, including the aforementioned divergence between high Andean, crevice-nesting *Muscisaxicola* species and Amazonian tree-nesting *M. fluviatilis*, and the vicariance between the high Andean, tree- and shrub-nesting *Polioxolmis-Cnemarchus* clade and the largely ground-nesting *Neoxolmis-Gubernetes* clade on lowlands to the east.

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APPENDIX 1

Vieillot's (1823) Latin and French description of *Tyrannus* (= *Neoxolmis*) *rufiventris*, which is based on Azara (1805) and Vieillot (1819), seems generally accurate and merits transcription here as a good general description of this species. Also presented is our own parallel English translation for the benefit of English-speakers.

****LE PEPOAZA A VENTRE ROUGEATRE. 5. T.**
Rufiventris. T. Guttur, jugulo corporeque suprâ plumbeis; subtùs rufo; caudâ nigricante, apice rufescente-fuscâ; rectricibus extimis albo marginatis; rostro pedibusque nigris.

Gorge, devant du cou et dessus du corps, plombés; dessous roux; queue noirâtre, terminée de brun-roussâtre; bec et pieds noirs.

On le rencontre dans les campagnes nues de Monte-Video; il marche avec agilité et célérité; fait à terre la chasse aux insectes et a le vol court et lent. La gorge, le devant du cou et ses côtés sont d'une teinte plombée claire, qui se rembrunit sur les parties supérieures; le sommet de la tête est noirâtre; le dessous du corps, rougeâtre; les plumes alaires sont de la même teinte en dessous, mais moins foncée en dessus, avec leur extrémité blanchâtre; leurs couvertures supérieures, d'un brun plombé et bordées de blanchâtre; la queue est noirâtre et terminée de brun-roussâtre, avec une bordure blanche à l'extérieur de sa première plume. *De Azara, Apuntamientos para la Hist. nat. de los Pajaros del Paraguay, etc. tom. 2. p. 172. n. 205. 2^e édit. du nouv. Diction. d'Hist. natur. tom. 35. p. 93. L'Amérique méridionale.*

L. 9 ½. E.. P. R. 12.

****THE REDDISH BELLIED PEPOAZA. 5. T.**
Rufiventris. Guttural Tyrant, throat and upper body plumbeous; underparts rufous; tail blackish, tip rufescent-brown; exterior rectrices white-edged; bill and feet black.

Throat, front of neck and upper body, plumbeous; underparts reddish; tail blackish, tipped in brown-reddish; bill and feet black.

It is met with in the barren countryside of Monte-Video; it walks with agility and speed; hunts insects on the ground and its flight is brief and slow. The throat, the front of neck and its sides are of a light plumbeous color, which become brown on the upper parts; the top of the head is blackish; the underpart of the body, reddish; the wing feathers are of the same color below, but less dark above, with their tip whitish; their upper coverts, a plumbeous brown and edged with whitish; the tail is blackish and tipped with brown-reddish, with a white edge on the outside of its first feather. *From Azara, Apuntamientos para la Hist. nat. de los Pajaros del Paraguay, etc. tom. 2. p. 172. n. 205. 2^e édit. du nouv. Diction. d'Hist. natur. tom. 35. p. 93. Southern America.*

L. 9 ½. E.. P. R. 12.

APPENDIX 2

Sight (1–70) and breeding records (71–79) of *Neoxolmis rufiventris* in Río Negro (71–75, 79) and Santa Cruz (1–34, 39–70, 76–78), Argentina, and in Magallanes (Region XII), Chile (35–38; see fig. 1). Sites 1–70 pertain to the 1993 American Museum of Natural History Patagonia Expedition; 71–76, to hitherto unpublished set slip data (appendix 3) in the egg collections of the Western Foundation of Vertebrate Zoology (71–73, 75), Santa Barbara Museum of Natural History (74), and Delaware Museum of Natural History (76); and 77–79, to previously published observations (Maclean, 1969, 1972, 1974; de la Peña, 1985, 1987, 1988; Vuilleumier, 1994).

(1) 15 Nov. 1993; Ruta 281, 17 km SE of Cerro Blanco and 4 km NW of Antonio de Biedma, ca. 47°29'S, 66°32'W; grassy steppe; 2 birds.

(2) 15 Nov. 1993; Ruta 281, 3 km SE of Antonio de Biedma and 16 km NW of Pampa Alta, ca. 47°31'S, 66°28'W; 18:10 hr; 2 birds.

(3) 16 Nov. 1993; ca. 10 km NW of Puerto Deseado, a few km S of Ruta 281 and SE of the Gruta de la Virgen de Lourdes, ca. 47°42'S,

65°59'W; very open steppe with cushionlike low shrubs predominating; 2 birds.

(4) 16 Nov. 1993; Ruta 2225, 3 km N of Ruta 281 and ca. 8 km NW of Tellier, ca. 47°37'S, 66°02'W; 17:45 hr; 1 bird.

(5) 16 Nov. 1993; Ruta 2225, 17–18 km N of Ruta 281 and ca. 22–23 km NNW of Tellier, ca. 47°30'S, 66°04'W; 1 bird.

(6) 16 Nov. 1993; Ruta 2225, 34 km N of Ruta 281 and ca. 39 km N of Tellier, ca. 47°22'S, 66°02'W; 2 birds.

(7) 16 Nov. 1993; Ruta 2221, 1 km E of Ruta 2225, 36 km N of Ruta 281 and ca. 41 km N of Tellier, ca. 47°21'S, 66°01'W; 2 birds.

(8) 17 Nov. 1993; Ruta 1201, 19 km SW of Tellier, ca. 47°46'S, 66°12'W; very open, bare pampa; 2 birds.

(9) 17 Nov. 1993; Ruta 1201, 16 km SSW of the Río Deseado, ca. 47°58'S, 66°42'W; 1 bird.

(10) 17 Nov. 1993; Ruta 1201, 21 km SSW of the Río Deseado, ca. 48°00'S, 66°43'W; 1 bird.

(11) 17 Nov. 1993; Ruta 1201, 49 km SW of the Río Deseado, ca. 48°06'S, 66°59'W; 2 birds.

(12) 18 Nov. 1993; Ruta 521, 84 km WNW of Hotel Bella Vista, ca. 48°55'S, 69°22'W; 310 m; very open steppe with short grass tussocks and low cushionlike shrubs on plateau; 18:20 hr; 2 birds.

(13) 18 Nov. 1993; Ruta 521, 54 km ESE of Gobernador Gregores, ca. 48°51'S, 69°38'W; 307 m; open steppe with very short grass and some low cushion shrubs; 2 birds.

(14) 18 Nov. 1993; Ruta 521, 42 km ESE of Gobernador Gregores, ca. 48°50'S, 69°44'W; ca. 350 m; flat grassy steppe; 19:05 hr; 1 bird.

(15) 18 Nov. 1993; Ruta 521, 10 km ESE of Gobernador Gregores, ca. 48°47'S, 70°07'W; very open short grass steppe; 1 bird.

(16) 19 Nov. 1993; Ruta 2310, 10 km W of intersection with Ruta 521 and ca. 20 km WSW of Gobernador Gregores, ca. 48°49'S, 70°30'W; very bare, boulder-strewn hillside with scattered cushion plants; 13:35 hr; 1 bird.

(17) 19 Nov. 1993; Ruta 2310, 10 km E of intersection with Ruta 40, ca. 48°52'S, 70°47'W; 420 m; flat, short grass steppe; 1 bird.

(18) 19 Nov. 1993; Ruta 2310, 2 km W of intersection with Ruta 40, ca. 48°52'S, 70°57'W; 420 m; very barren short grass and cushion plant steppe; 1 bird.

(19) 19 Nov. 1993; Ruta 2310, 4 km W of intersection with Ruta 40, ca. 48°52'S, 70°58'W; very barren short grass and cushion plant steppe; 1 bird.

(20) 19 Nov. 1993; Ruta 2310, 5 km W of intersection with Ruta 40, ca. 48°52'S, 70°59'W; very barren short grass and cushion plant steppe; 1 bird.

(21) 19 Nov. 1993; Ruta 2310, 6 km W of intersection with Ruta 40, ca. 48°52'S, 71°00'W; 440 m; barren steppe with grass tussocks, very low shrubs, and much bare ground; 18:15 hr; 1 bird.

(22) 19 Nov. 1993; Ruta 2310, 4 km W of intersection with Ruta 40, ca. 48°52'S, 70°58'W; 440 m; short grass and cushion shrub steppe; 18:23 hr; 1 bird.

(23) 19 Nov. 1993; Ruta 2310, 3 km W of intersection with Ruta 40, ca. 48°52'S, 70°57'W; 420 m; short grass and low cushion plant steppe; 2 birds.

(24) 19 Nov. 1993; Ruta 2310, 1 km W of intersection with Ruta 40, ca. 48°52'S, 70°56'W; 410 m; short grass and low cushion plant steppe; 1 bird.

(25) 19 Nov. 1993; Ruta 2310, 8 km E of intersection with Ruta 40, ca. 48°52'S, 70°49'W; 390 m; short grass steppe with few cushions; 1 bird.

(26) 19 Nov. 1993; Ruta 2310, 15 km E of intersection with Ruta 40, ca. 48°52'S, 70°43'W;

410 m; short grass and cushion shrub steppe; 19:10 hr; 1 bird.

(27) 21 Nov. 1993; Ruta 1301, 26 km S of Gobernador Gregores, on right bank of the Río Chico, ca. 48°55'S, 70°16'W; 270 m; very barren, overgrazed and trampled short tussock grass steppe with low cushion plants on floodplain; 11:30–13:00 hr; 2 birds.

(28) 21 Nov. 1993; Ruta 1301, 13 km NNW of intersection with Ruta 288, on right bank of the Río Chico, ca. 49°29'S, 69°37'W; 140 m; low tussock grass steppe with much bare ground; 16:45–17:40 hr; 2–3 birds.

(29) 21 Nov. 1993; Ruta 1301, 11 km NNW of intersection with Ruta 288, on right bank of the Río Chico, ca. 49°31'S, 69°37'W; 130 m; tussock grass steppe with extensive bare areas; 18:55 hr; 1 bird.

(30) 21 Nov. 1993; Ruta 288, 31 km SE of intersection with Ruta 1301, ca. 49°42'S, 69°16'W; 165 m; shrubsteppe-tussock grass association on plateau; 19:35 hr; 1 bird.

(31) 21 Nov. 1993; Ruta 288, 48 km SE of intersection with Ruta 1301 and 27 km NNW of Cmte. Luis Piedra Buena, ca. 49°45'S, 69°11'W; 155–160 m; low open shrubsteppe; 19:50 hr; 1 bird.

(32) 22 Nov. 1993; Ruta 3, 81 km SSW of intersection with Ruta 288 and 13 km NNE of Hotel Le Marchand, ca. 50°40'S, 69°23'W; ≤ 300 m; fairly dense shrubsteppe; 13:15 hr; 1 bird.

(33) 23 Nov. 1993; Ruta 3, near Ea. Don Bosco, 32 km SSW of Río Gallegos, 29 km NNE of Laguna Azul access road, and 39 km NNE of Monte Aymond (Paso de Integración Austral), ca. 51°52'S, 69°26'W; 100 m; very open, short grass steppe; 12:20 hr; 1 bird.

(34) 23 Nov. 1993; Ruta 3, 33 km SSW of Río Gallegos, 28 km NNE of Laguna Azul access road, and 38 km NNE of Monte Aymond (Paso de Integración Austral), ca. 51°52'S, 69°26'W; 100 m; very open, short grass steppe; 12:30 hr; 1 bird.

(35) 23 Nov. 1993; Ruta 255 CH, 7 km S of Monte Aymond (Paso de Integración Austral), ca. 52°12'S, 69°29'W; 140 m; overgrazed steppe; 1 bird.

(36) 23 Nov. 1993; unnumbered road, ca. 12 km N of Punta Delgada (O'Higgins), ca. 52°14'S, 69°44'W; 230 m; lush grass steppe on plateau; 20:20 hr; 1 bird.

(37) 23 Nov. 1993; unnumbered road, 3 km N of Punta Delgada (O'Higgins), ca. 52°19'S, 69°41'W; 130 m; shrubsteppe in stream valley; 21:00 hr; 1 bird.

(38) 27 Nov. 1993; Ruta 257 CH, 3 km E of Sombrero exit, ca. 52°44'S, 69°18'W; 60 m; vast grassland; 17:45 hr; 1 bird.

(39) 30 Nov. 1993; Ruta 7, 12 km WSW of intersection with Ruta 5, ca. 51°04'S, 70°56'W; 400 m; tussock grass and low shrub steppe association on terrace; 13:25 hr; 1 bird.

(40) 30 Nov. 1993; Ruta 7, 13 km WSW of intersection with Ruta 5, ca. 51°04'S, 70°57'W; 415 m; tussock grass and low shrub steppe association on terrace; 13:35 hr; 1 bird.

(41) 30 Nov. 1993; Ruta 7, at Ea. Luján exit, 14–15 km WSW of intersection with Ruta 5, ca. 51°03'S, 70°59'W; ca. 400 m; grass and shrub association on N face of Río Coig (Coyle) terrace; 13:45 hr; 2 birds.

(42) 30 Nov. 1993; Ruta 7, 19 km E of Ea. Tapí Aike and Río Coig (Coyle) crossing, ca. 51°03'S, 71°33'W; 540 m; grazed short grass steppe with scattered low cushion shrubs in low, rolling hills (moraines?) S of the Río Coig; 17:10 hr; 1 bird.

(43) 1 Dec. 1993; Ruta 40, 24 km NE of Fuentes del Coyle, ca. 51°00'S, 71°43'W; 600 m; short grass steppe; 14:05 hr; 1 bird.

(44) 1 Dec. 1993; Ruta 40, 26 km NE of Fuentes del Coyle, ca. 50°58'S, 71°42'W; 600 m; grazed tussock grass steppe; 14:10 hr; 1 bird.

(45) 1 Dec. 1993; Ruta 40, 40 km NE of Fuentes del Coyle, ca. 50°53'S, 71°33'W; 705 m; hummocky grass steppe; 15:55 hr; 2 birds.

(46) 1 Dec. 1993; Ruta 40, 41 km NE of Fuentes del Coyle, ca. 50°53'S, 71°32'W; 700 m; grazed tussock grass steppe in valley; 16:05 hr; 1 bird.

(47) 1 Dec. 1993; Ruta 40, 57 km NE of Fuentes del Coyle, ca. 50°46'S, 71°29'W; 735 m; short grass steppe with fairly numerous shrubs; 16:45 hr; 1 bird.

(48) 1 Dec. 1993; Ruta 40, 71 km NE of Fuentes del Coyle and 13 km SSW of El Cerrito, ca. 50°43'S, 71°24'W; 740 m; plateau with fairly dense shrubs (to 1 m tall) and short grasses; 17:15 hr; 1 bird.

(49) 1 Dec. 1993; Ruta 40, E of Ea. La Porteña and 13 km SE of the southernmost Laguna Los Escarchados exit, ca. 50°31'S, 71°26'W; 920 m; gravelly roadside with sparse tussocks; 18:20 hr; 1 bird.

(50) 4 Dec. 1993; Ruta 40, between Lago Argentino and Lago Viedma on W bank of the Río La Leona, 33 km NNW of the Ruta 40 crossing of Río La Leona near the E end of Lago Argentino, and 20 km S of the Ruta 40 crossing of Río La Leona near the E end of Lago Viedma, ca. 49°59'S, 72°05'W; 250 m; grazed short grass and low cushion steppe on alluvial fan next to escarpment in valley; 14:10 hr; 2 birds.

(51) 4 Dec. 1993; New Ruta 288, 11 km ENE of Tres Lagos, ca. 49°35'S, 71°18'W; 300 m; short

grass steppe with low cushion shrubs; 19:25 hr; 1 bird.

(52) 4 Dec. 1993; Ruta 67, 2 km S of the Río Shehuen (Chalía) and 4 km S of Old Ruta 288, ca. 49°36'S, 71°10'W; 240 m; very bare, overgrazed grass steppe on floodplain; 21:20 hr; 1 bird.

(53) 4 Dec. 1993; left bank of the Río Shehuen (Chalía) near intersection of Ruta 67 with Old Ruta 288, ca. 49°34'S, 71°11'W; 250 m; low tussock grass and cushion plant steppe on alluvial plain; 21:30 hr; 1 bird.

(54) 5 Dec. 1993; Ruta 40, 4 km NW of Tres Lagos, ca. 49°35'S, 71°29'W; 265 m; sparse tussock grass and cushion plant steppe on plateau; 11:00 hr; 1 bird.

(55) 5 Dec. 1993; Ruta 40, 18 km NW of Tres Lagos, ca. 49°30'S, 71°35'W; 380 m; dense tussock grass and shrub steppe; 11:15 hr; 1 bird.

(56) 5 Dec. 1993; Ruta 40, 4 km NE of intersection with Ruta 29 (2310), ca. 48°51'S, 70°52'W; 400 m; rather bare short grass and cushion plant steppe; 16:35 hr; 1 bird.

(57) 5 Dec. 1993; unnumbered road, 1 km E of Ruta 40 and 13 km NE of Ruta 40-Ruta 29 (2310) intersection, ca. 48°49'S, 70°47'W; 375 m; rather bare short grass steppe on plateau; 17:00 hr; 2 birds.

(58) 5 Dec. 1993; unnumbered road, 2 km E of Ruta 40 and 13 km NE of Ruta 40-Ruta 29 (2310) intersection, ca. 48°50'S, 70°46'W; ca. 375 m; rather bare short grass steppe on plateau; 17:15 hr; 1 bird.

(59) 6 Dec. 1993; Ruta 40, 29 km NE of Hotel Las Horquetas, ca. 48°03'S, 71°02'W; 600 m; short grass steppe with widely spaced shrubs; 10:35 hr; 1 bird.

(60) 6 Dec. 1993; Ruta 40, 41 km NE of Hotel Las Horquetas and 41 km SW of the Río Olnie, ca. 47°58'S, 70°57'W; 640 m; short grass steppe; 10:50 hr; 2 birds.

(61) 6 Dec. 1993; Ruta 40, 29 km S of the Río Olnie, ca. 47°53'S, 70°52'W; 690 m; short grass steppe; 11:05 hr; 2 birds.

(62) 6 Dec. 1993; Ruta 40, 28 km S of the Río Olnie, ca. 47°52'S, 70°51'W; 690 m; short grass steppe; 11:10 hr; 2 birds.

(63) 6 Dec. 1993; Ruta 40, 27 km S of the Río Olnie, ca. 47°52'S, 70°51'W; 700 m; short grass steppe; 11:15 hr; 1 bird.

(64) 6 Dec. 1993; Ruta 40, 25 km S of the Río Olnie, ca. 47°51'S, 70°50'W; 720 m; short grass steppe; 11:30 hr; 1 bird.

(65) 6 Dec. 1993; Ruta 40, 20 km S of the Río Olnie, ca. 47°49'S, 70°49'W; 730 m; short grass and shrubsteppe mosaic in valley; 11:35 hr; 4 birds.

(66) 6 Dec. 1993; Ruta 40, 16 km S of the Río

Olnie, ca. 47°47'S, 70°50'W; 760 m; short tussock grass steppe with some low shrubs; 11:50 hr; 2 birds.

(67) 6 Dec. 1993; Ruta 40, 23 km NNW of Bajo Caracoles and 27 km SSW of the Río Ecker, ca. 47°18'S, 70°58'W; 580 m; short grass steppe; 15:00 hr; 1 bird.

(68) 6 Dec. 1993; Ruta 40, 10 km SSE of Perito Moreno, ca. 46°41'S, 70°53'W; 470 m; low tussock grass and shrub steppe; 17:35 hr; 1 bird.

(69) 7 Dec. 1993; Ruta 40, 30 km NNE of intersection with Ruta 43 and 44 km SW of the Provincia del Chubut border crossing, ca. 46°18'S, 70°45'W; 800 m; moderately tall grass and shrub steppe on hillslope; 12:55 hr; 1 bird.

(70) 7 Dec. 1993; Ruta 40, 31 km NNE of intersection with Ruta 43 and 43 km SW of the Provincia del Chubut border crossing, ca. 46°17'S, 70°45'W; 780 m; moderately tall grass and shrub steppe on hillslope; 13:00 hr; 1 bird.

(71) 1 Nov. 1911; Ea. Huanu-Luan, 88 km WSW of Maquinchao (Paynter, 1995: 327), ca. 41°22'S, 69°52'W; high plateau; nest containing 2 half-incubated eggs (WVZ 15164).

(72) 9 Nov. 1911; near Cerro Añecón Grande, 90 km ESE of San Carlos de Bariloche (Paynter, 1995: 29), ca. 41°25'S, 70°16'W; hillside in basalt mesa country; 1600 m; parent bird; nest containing 2 piped eggs (WVZ 15165).

(73) 10 Nov. 1911; Ea. Huanu-Luan, 88 km WSW of Maquinchao (Paynter, 1995: 327), ca. 41°22'S, 69°52'W; hillside; nest containing 2 piped eggs (WVZ 15166).

(74) 23 Dec. 1911; Arroyo Añecón Grande on northern slope of Cerro Añecón Grande (Paynter, 1995: 29), ca. 41°08'–41°25'S, 70°11'–70°24'W;

high mesa bordering arroyo; parent bird; nest containing 2 fresh eggs (SBMNH 166-25).

(75) 31 Dec. 1911; Arroyo Añecón Grande on northern slope of Cerro Añecón Grande (Paynter, 1995: 29), ca. 41°08'–41°25'S, 70°11'–70°24'W; 2.4 m from level surface in crevice of vertical rock wall; deserted nest containing 1 rotten egg (WVZ 15167).

(76) 25 Oct. 1933; Ea. Condor (= "Ea. El Cóndor"; Ejército Argentino, 1948a), ca. 16–64 km S of Río Gallegos (Paynter, 1995: 228–229; A. T. Waldron, personal commun.; Charles Bingham, personal commun.), ca. 52°10'S, 69°04'W; ca. 100 m (Paynter, 1995: 228); open "camp" under a tuft of grass; nest containing 2 eggs (cited as "*Myiotheretes striaticollis*" by Kiff and Hough, 1985: 106; DMNH 23722).

(77) 3–4 Dec. 1967; Ea. Las Vegas (Paynter, 1995: 423; Ejército Argentino, 1948b), ca. 51°40'S, 71°30'W (Gordon L. Maclean, personal commun.); W slope of small dry wash leading into valley of the Río Coyle; flat, open pampa with sparse grass, some low woody shrubs and occasional *Berberis* bushes; incubating parent bird; nest containing 3 eggs (Maclean, 1969, 1972, 1974, personal commun.; AWJ).

(78) 7 Nov. 1979; Puerto Deseado (Paynter, 1995: 618–619), ca. 47°45'S, 65°54'W; nest containing 1 nestling and 2 unincubated eggs (de la Peña, 1985, 1987, 1988; MRDLP 379).

(79) 7 Nov. 1992; ca. 20 km E of El Cañal at W base of Meseta de Somuncurá (Paynter, 1995: 223), ca. 41°40'S, 67°54'W; ca. 1100 m; open steppe with 20–30 cm tall shrubs and tussock grass; 2 parent birds; nest containing 2 large young (Vuilleumier, 1994).

APPENDIX 3

Data on eggs and nests of *Neoxolmis rufiventris* from set slips in the collections of J. R. Pemberton (WVZ 15164–15167, SBMNH 166-25) and A. T. Waldron (DMNH 23722).

WVZ 15164. "Set number . . . 457. No. of eggs . . . 2. Date . . . November 1, 1911. Locality . . . Huana Luan, F.C.P., Río Negro, Argentina. Collector . . . Peon in employ [of] J. R. Pemberton. Incubation . . . About ½ incubated. Nest . . . Made of dry grass loosely thrown together - lining - a few large filmy ostrich feathers. Placed upon high plateau, sheltered behind rock - placed on ground. Remarks . . . Bird unknown to me so far. Peon thought it was a dove. [Addendum:] Later sets 469 & 478 are of same bird which was well identified. Cat. # 102 Spec. # 76 & 77."

WVZ 15165. "Set number . . . 478. No. of eggs . . . 2. Date . . . November 9, 1911. Locality . . . Near Cerro Anecon Grande, altitude nest, 1600 meters, F.C.P., Río Negro, Argentina. Collector . . . J. R. Pemberton personally. Identity . . . Bird flushed from nest. Incubation . . . Piped [sic] & ready to hatch. Nest . . . Well made nest of dry grass, lined with a profusion of ostrich feathers. Placed on ground at base of tussock of grass. Located on hill side in basalt mesa country. Remarks . . . Robin [sic]. Cat. # 102 Spec. # 76–77. Same as set # 457."

WVZ 15166. "Set number . . . 469. No. of eggs . . . 2. Date . . . November 10, 1911. Locality . . . Huana Luan, F.C.P., Río Negro, Argentina. Collector . . . Peon, in camp; for J. R. Pemberton.

Identity . . . Bird described & eggs known by m[e?]. Incubation . . . Ready to hatch - piped [sic] in fact. Nest . . . Placed on ground at foot of a small tussock of grass, well up on side hill. Made of dry grass and lined with great amount of ostrich feathers. Remarks . . . Robin [sic] of my list. Cat. # 102 Spec. # 76 & 77. Same as set # 457."

SBMNH 166-25. "Set number . . . 521. No. of eggs . . . 2. Date . . . December 23, 1911. Locality . . . Arroyo Anecon Grande, F.C.P., Rio Negro, Argentina. Collector . . . J. R. Pemberton personally. Identity . . . Bird flushed from nest. Incubation . . . Perfectly fresh. Nest . . . Placed on ground at base, leeward side, of large tuft of grass; on high mesa bordering arroyo. Made of large amount of dry grasses and fine twigs. Deep cup interior deeply lined with feathers only. Remarks . . . Robin [sic]. Cat. # 102 Spec. # 76-77."

WFVZ 15167. "Set number . . . 544. No. of eggs . . . 1. Date . . . December 31, 1911. Locality . . . Arroyo Anecon Grande, Rio Negro, Argentina. Collector . . . J. R. Pemberton personally. Identity . . . Evident from egg. Incubation . . . Rotten egg, deserted nest. Nest . . . Made of sticks, straw and wool principally with lining of feathers. Placed 8 feet from level surface in crevice in vertical rock wall. Remarks . . . Robin [deleted]. Cat. # 102 Spec. # 76 & 77. Same as set # 457."

DMNH 23722. "Collected by . . . A. T. Waldron on . . . 25 October [19]33 at . . . Estancia Condor, Rio Gallegos. No. of eggs in set . . . 2 . . . Nest . . . In the open camp under a tuft of grass. Lined with grass & feathers. Fairly common but never seen here more than a pair together. A very pretty bird with a flight somewhat resembling a thrush. Have never heard them make any sort of call."

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